TRANSACTIONS AND PROCEEDINGS

OF THE

BOTANICAL SOCIETY OF EDINBURGH.

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TRANSACTIONS AND PROCEEDINGS

OF THE

BOTANICAL SOCIETY OF EDINBURGH.

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TRANSACTIONS

OF THE

BOTANICAL SOCIETY OF EDINBURGH

SESSION CXII

POTAMOGETONS IN THE SCOTTISH WESTERN ISLES, WITH SOME REMARKS ON THE GENERAL NATURAL HISTORY OF THE SPECIES.

By J. W. HESLOP HARRISON, D.Sc., F.R.S.

(Read 15th May 1947.)

In the past, owing to the difficulty of understanding its various species, the genus Potamogeton has attracted very little attention in this country, although the pioneer work of Fryer and Bennett should have formed a very valuable basis for subsequent investigations. This difficulty depended not merely upon the general similarity of many of the species, but also upon two other factors. In the first place, due to the ease with which individual plants respond to environmental influences, the fluctuating variation within the species covers an enormous and bewildering range of forms. It is most tempting to regard the most extreme of these variants as fully worthy of special names; nevertheless, when one assembles a number for study and comparison, the whole reveals itself as a regular series, puzzling it is true, but with its individuals merging insensibly in facies into each other. Further, with the exception of the members of the water-pollinated subgenus Coleogeton, the Potamogetons are wind-pollinated. Since the species tend to be gregarious, and the flowering spikes to protrude much the same height above the surface of the water, a great amount of interspecific pollination is rendered possible, thereby bringing about a great deal of hybridity with a consequent masking of the true limits of species. Similarly, within the ranks of Coleogetons, the distribution of pollen into the water also results in the free production of hybrid swarms, and thus adds to the perplexities presented by that subgenus.

However, on the whole, careful study leads to an understanding of at least the fertile representatives of the genus, and their true relationships. On the other hand, not only are masses of sterile hybrids encountered, but, in addition, certain genuine species appear to be shy fruiters in some of their habitats. Fortunately, during the present century, several exceptionally capable workers have tackled the whole of the problems of the genus, and have produced order out of what was previously little better than chaos. Of such investigators, Hagström, Fernald, Pearsall and Ogden deserve special mention for the general accuracy and comprehensiveness of their work, and to them we owe the stimulus which caused us to approach the study of Hebridean Potamogetons with energy and zeal.

Our labours with the pond-weeds of the Scottish Western Isles commenced in 1934 on the isles of Raasay and South Rona. Since then they have been extended to include most of the islands comprised in the Watsonian vice-counties 102, 103, 104 and 110. At an early stage, we gained the impression that the Hebrides were very poor in Potamogetons, for loch after loch was examined and found to produce nothing more than the ubiquitous *Potamogeton natans* and *P. polygonifolius*. Once the Outer Isles came into the picture, our views underwent a complete change, for there the lochs examined in the early stages of our work were prolific, not only in species, but also in individuals. These lochs were machair lochs, and when we left them to work lochs in the transition zones between machair and moorland, and the moorland lochs and lochans themselves, we found that the number of Potamogetons encountered fell off steeply. Indeed, in the moorland lochs little was observed except *P. natans*, *P. polygonifolius* and, occasionally, *P. Millardii* subsp. *lacustris* Pearsall and Pearsall f. Moreover, on South Uist and elsewhere, it was quite possible to find a sheet of water with its Potamogeton flora of the machair type at one end, and of the type characteristic of moorland waters at the other. Obviously, the comparatively shallow machair loch, with its sandy bottom and the presence of unlimited calcareous sand, favours the growth of pond-weeds; on the other hand, moorland lochs, with rocky beds and more acid conditions, prove much more unsuitable. Although there can be no doubt that the plants present in any given habitat, as well as the pH of that habitat, depend upon the interaction of many factors, it appears certain that there is some degree of correlation between the Potamogeton flora of a loch and the pH value of its waters.

Commencing with brackish lochs of very high pH values, we find them for the most part yielding only *Potamogeton pectinatus* and, occasionally, *P. filiformis*. However, the machair lochs are marked by a change; their waters exhibit a pH range of 6·5 to 7·75 and their Potamogeton tenants, whilst varying from loch to loch, are strong in individuals and represent many species. On the contrary, as one passes to the moorlands, where the waters usually become more acid and display lower pH values, the pond-weed populations become impoverished, until only *P. natans* and *P. polygonifolius* are able to withstand the conditions. Once these facts were recognized, lochs on the Inner Isles, reproducing to a greater or less extent the conditions of a typical machair loch, were marked out on our maps, and examined. Invariably, as on the isles of Coll and Tiree, such lochs yielded the same forms as similar sheets of water in the Outer Isles. On the isle of Rhum, only two lochs, Loch Papadil and Loch Fiachanis, offer any resemblance to such lochs; as expected, they too supported a wealth of Potamogetons.

In spite of such observations, it must not be supposed that the rarer pond-weeds are invariably restricted to machair lochs; at times, as on Skye, Rhum, Raasay and Coll, local circumstances cause moorland lochs to produce a selection of unexpected species although, as a general rule, only one or two species are involved. Thus on the isle of Raasay, Loch na Meilich (pH 7·3), lying on Jurassic rocks, yields both *P. praelongus* and *P. lucens*.

It is necessary to point out that with the exception of certain species, collected in Raasay and Skye, which were determined by the late W. H. Pearsall, to whom we are very grateful for many favours, the whole of our material was identified by ourselves.

Subgenus **Eupotamogeton** Raunk.

Potamogeton natans L.

Except for *P. polygonifolius*, this species is the most abundant and widely distributed pond-weed in the Inner and Outer Hebrides. Further, it is the most accommodating in its needs, for it seems just as much at home in the machair lochs at sea-level as it is in lochs on the moorlands and high up in the hills. In addition, it abounds in all streams of suitable depth.

Localities.—v.-c. 102, Colonsay; 103, Coll and Tiree; 104, Skye, Raasay, South Rona, Scalpay, Rhum, Eigg, Muck; 110, Lewis and Scarp to Sandray, abundant.

pH Values of Typical Habitats.—Loch an Duin, Coll, 5·1; Loch Olivat, Benbecula, 5·5; Loch Scotageary, Barra, 5·8; Loch Ollay,

S. Uist, 6; Loch Papadil, Rhum, 6·4; Loch Uachdair, Raasay, 6·9; Loch Eadar da Bhaile, Raasay, 7·2; Loch Rathaid, Raasay, 7·8; Loch Chadacharnaich, Raasay, 8·2.

Although the pH values supplied show the range tolerated by *P. natans*, they tend to mask one or two important facts. Whilst the species cannot be described as acidiphilous, nevertheless, except for *P. polygonifolius*, it is the first pond-weed to appear in waters of lower pH ranges. As a result, in moorland lochs and other sheets of water in which such pH values prevail, it forms the sole pond-weed tenant. This, however, does not imply that it is not quite at home in the alkaline waters from which we have recorded it.

The times at which *P. natans* begins its growth vary greatly with the habitat. Thus, in a pool nearly three feet deep, kept under observation, no growth was discernible on 2nd February 1945, only last year's phyllodes being present. Close by, however, in a shallow pool with a clayey bottom, not only were last year's leaves preserved but, further, a few newly-expanded, brown floating leaves were observed. In the deeper pool, the first floating leaves only began to unfold on 10th April. None the less, both series of plants were in full leaf and just commencing to flower on 23rd May. By 1st July, both fruits and a second succession of flowers were present. Fruits were collected later in the season, and placed in the aquarium. No seeds germinated during the first year, and all were destroyed finally by algal growths.

In the Hebrides, wild ducks and other water-birds feed greedily on the fruits, and swans tear up its rhizomes for food. Of the usual aquatic insects, various species of Trichoptera, as well as the larvae of the China Mark Moth, *Hydrocampa nymphaeata*, consume its leaves. It is interesting, too, to note that, on one occasion, the caddis-fly, *Leptocerus aterrimus*, as well as various Diptera, were seen at its flowers; what the insects were obtaining was not ascertained.

As has been made clear above, *P. natans* may be found alone in many moorland pools in the Hebrides. In others, it may be accompanied by additional species like *Myriophyllum spicatum* or *Lobelia Dortmanna*. Occasionally, even in moorland lochans, quite a rich flora may be associated with it, as in Loch Fada on Grimsay, where *Nymphaea alba*, *Littorella uniflora*, *Utricularia minor*, *Lobelia Dortmanna*, *Sparganium angustifolium*, *Equisetum limosum* and *Nitella opaca* were noted. In the adjacent isle of Ronay a small loch exhibited the same selection, with the addition of *Scirpus Tabernaemontani* and *Phragmitis communis*. On the isle of Coll, in

Loch a' Mhill Aird, it appeared in a very interesting assemblage composed of *P. gramineus*, *Nymphaea alba*, *Lobelia Dortmanna*, *Myriophyllum spicatum*, *Menyanthes trifoliata*, *Littorella uniflora*, *Apium inundatum*, *Baldellia ranunculoides*, *Eriocaulon septangulare*, *Eleocharis palustris*, *Scirpus fluitans* and *Carex rostrata*. For other associations, chiefly in machair lochs, reference may be made to the lists given for other species.

Potamogeton polygonifolius Pourr.

This species is by far the most abundant pond-weed in the Hebrides, for it may be found in every island. In its habitats, whilst manifesting a wide diversity of choice, it seems to prefer moorland slacks and hollows, although it occurs freely in ditches, streams and lochs. Under such circumstances it shows a wide spread of variation, which reaches its maximum when the plant grows in water. Thus in a lochan near Loch Uamadale, isle of Harris, with a peaty bottom, it produces long, narrow, pellucid leaves, whilst in Lochs Sgaorishal and Fiachanis, isle of Rhum, the former with a rocky bottom and the latter more or less sandy, lanceolate, pellucid leaves, brown in colour, and strongly recalling those of *P. alpinus*, are developed. In both of these lochs it shuns the margins and flourishes in the deeper water. On the same island, in a deep stretch of a stream at an elevation of 750 feet on Bloodstone Hill, a very remarkable and beautiful form, the variety *cancellatus* Fryer, hitherto recorded only from the Shetland Isles, is encountered; this plant fills the stream for over one hundred yards. Elsewhere, the variation provokes but little comment, except that it should be pointed out that some Sandray (v.-c. 110) specimens have rounded, smallish leaves. In assigning a cause for such a spread of variation as that just detailed, no doubt appeal should be made to environmental agencies in the first place; nevertheless, protracted field studies have led to the view that some of it is genetical in its origin.

P. polygonifolius starts into growth early in the year; thus plants growing in nine inches of water, and still carrying the foliage of the preceding year, exhibited new shoots three inches long on 27th February 1945, and the first flowers appeared on 23rd May. Ripe fruits were obtainable throughout August, September and October.

Most of the remarks on the relations between animals and *P. natans* apply to this species, but it seems worthy of note that, early in June 1942, larvae of the Common Tiger Moth (*Arctia caja*) were seen feeding on the leaves of *P. polygonifolius* in a small stream north of Lochboisdale, S. Uist.

Very often, even when land forms are concerned, *P. polygonifolius* grows in "pure stands." Generally, however, in moorland localities, it has for companions the usual plants characteristic of such areas. In lochs it appears in a variety of associations, most of which are restricted in the number of species represented. On the isle of Rhum, in Loch Fiachanis, there grow with it *Myriophyllum spicatum*, *Potamogeton gramineus*, *P. perfoliatus*, and *P. Millardii*; on the other hand, in a loch behind Gullan na Pairce, in the same island, its neighbours are *Lobelia Dortmanna* and *Eriophorum angustifolium*. In the lower reaches of Loch Ollay, S. Uist, it flourishes alongside *Ranunculus trichophyllus*, *Nymphaea alba*, *Myriophyllum spicatum*, *P. gramineus* and *Sparganium angustifolium*. On Coll, in a little runnel flowing into Loch a' Mhill Aird, it has most unusual neighbours: *Baldellia ranunculoides* and *Eriocaulon septangulare*. When it occurs in the machair lochs of the Outer Isles it often forms a fringe on the shoreward side of the associations listed in the accounts of other species.

pH Values typical of its Habitats.—Moorland slack, Minish, Benbecula 4·4; moorland hollows, Small Isles, 4·8; runnel near Loch a' Mhill Aird, 4·9; lochan near Loch Ceann a' Bagh, S. Uist, 5·8.

× **Potamogeton Gessnacensis** Fischer (= **P. natans** × **P. polygonifolius**)

After careful study, a very puzzling plant, collected in August 1947, in Loch na Liana Moire, Benbecula, was determined as a representative of this hybrid. It grew amongst its putative parents.

Potamogeton coloratus Hornem.

This rather striking pond-weed is of sparse occurrence in the Hebrides.

Localities.—v.-c. 103, in a tank on Balephetrish Hill, Tiree, Lochan a' Chuirn, Coll; 104, lochan in Glen Shellesder, Rhum; 110, Loch Sniogravat, Monach Isles, Loch na Liana Moire, Benbecula.

pH Values of the Benbecula Station.—Loch na Liana Moire lies in the machair-moorland transition zones, and the pH values of its waters vary between 6·9 and 7·1.

Benbecula plants of *P. coloratus* removed to my garden pond for observation came into leaf early in February, and it soon became clear that, for the most part, the various stages in its life-history synchronized with those of *P. polygonifolius.* Thus, in August 1944, 1946 and 1947, the wild plants of both species in Loch na Liana Moire bore quantities of ripe fruit which continued to be set free for a fairly long period. Certain plants of *P. coloratus*, placed in my pond in 1944, shed the bulk of their fruits on 2nd September; these kept floating until 9th September, when, one by one, they commenced to sink.

On 4th February 1945 four seeds were seen to have germinated, but no more did so until the period 30th March–8th April, when a succession of seedlings appeared. After that there was a break for a week, with germination recommencing on 15th April and continuing irregularly until late in June. The earliest seedlings displayed their first foliage leaves on 12th April.

In its Tiree station its sole companion is *P. polygonifolius*, but in Lochan a' Chuirn it is accompanied by *P. gramineus*, *P. Millardii*, *Myriophyllum spicatum* and *Baldellia ranunculoides.* In Loch na Liana Moire, where it is very abundant, we have, by means of wading operations, made detailed observations on its habitats; these examinations have caused important changes in the impressions gained in 1940. Although the plant occurs everywhere in the loch except in the north, north-east, and in deep water, probably the three best localities are that in which it was originally discovered along the western shore, a second in a little cove in the south-east and a third to the west of the drainage lode flowing from the south. In the first-mentioned station it occupies a belt of very sticky mud lying between *P. filiformis*, growing in shallow water, and *Polygonum amphibium* furthest from the shore. In the second locality, where it is easily overlooked, it grows intermingled with a little *Myriophyllum* and *Littorella*, in the angle between a mixed colony of ×*P. sparganifolius* and ×*P. Billupsii* and a dense mass of *Phragmites communis.* To the north-west it meets *P. natans* and, rarely, *P. pectinatus* and *Chara hispida*, whilst there is a slight reciprocal transgression between it and the hybrids. Here, it seems to prefer depths between six and eighteen inches, although seedlings in various stages may be found close into the shore. At its third station, where the bottom is decidedly stony, the arrangement differs. On the shoreward side we encounter the two hybrids already mentioned, followed by an intimate mixture of *P. coloratus* and *P. natans.* To the west the coast sweeps sharply northward, and between it and the mixed colony succeeds a growth of *P. natans* with which may be seen a little ×*P. sparganifolius*. The whole is enclosed by a crescent-shaped band of *Eleocharis palustris*, but within that band, at any point, small amounts of *Myriophyllum* and *Littorella* are liable to occur.

×**Potamogeton Billupsii** Fryer (=**P. gramineus**×**P. coloratus**)

Prior to our discovery of *P. Billupsii* on Benbecula (v.-c. 110), it had been recorded only from two British stations, one at Benwick, Cambs., and the other in Wood Walton Fen, Hunts.

In our locality the plant is extremely plentiful, and very uniform in facies. Further, except that Fryer's examples appear to be a little longer both in the upper and the lower leaves than ours, his Plate 338 (*Journ. Bot.*, xxxi, p. 353) could readily have been drawn from Benbecula specimens. However, if one may judge from his remarks, his plants were much shyer in flowering than ours. Like those of Fryer's series, our examples are quite sterile, and rarely expand their flowers.

As the outcome of careful study of ×*P. Billupsii* and its neighbours in nature, we can state, despite the decadence of *P. gramineus* in the loch, that the parentage is as given. Moreover, although we have never observed *P. gramineus* in flower or fruit in Loch na Liana Moire, we are equally certain that the exact parentage is *P. gramineus* ♀×*P. coloratus* ♂. This conclusion depends upon the fact that, whilst only rarely does one find *P. Billupsii* growing near *P. coloratus*, it is often found alongside *P. gramineus*.

×*P. Billupsii* covers considerable areas of the loch, a fact depending in the main on the effects of heterosis acting in conjunction with excessive vegetative reproduction. In addition, it appears obvious that, unless some of the colonies originate in the dispersal of broken fragments by wave action, the hybrid has arisen as the result of several independent cross pollinations. In favour of the latter view may be advanced the fact that examinations of the "wash" along the shores have always failed to reveal such fragments.

Reference to the account of *P. coloratus* will supply the necessary facts concerning the usual associates of ×*P. Billupsii*.

Potamogeton lucens L.

In this species we are concerned with a plant rarely reported from the Western Isles. In point of fact, records exist for two vice-counties only, v.-c. 104 and v.-c. 110. In the former area we have been able to examine specimens from two localities, one, where it exists in such quantities as to be a nuisance to anglers, is the Storr Lochs on Skye, and the other Loch na Meilich, on Raasay.

Considerable doubt exists in connection with its status in the Outer Isles. In fact, although Druce records it for v.-c. 110 in the Comital Flora, no one seems to be cognizant of the source of his information. Again, the Edinburgh workers (*Proc. Roy. Phys. Soc.*, xxii, p. 250) list it, with *P. praelongus*, from Loch an Duin, isle of Barra, but this has never been confirmed. Our explorations have only resulted in the detection of a small colony in a drainage stream near Loch Kildonan, South Uist, where it had no associates.

In Loch na Meilich, Raasay (pH 7·3), it was accompanied by *P. praelongus*, but there were also present *Myriophyllum spicatum* and *Sparganium angustifolium*.

Potamogeton gramineus L.

This species occurs more abundantly in the Outer Isles than in the Inner group, although we have discovered recently that its range in v.-cs. 102, 103 and 104 is greater than we had supposed.

Localities.—v.-c. 102, Lochs Fada and Sgoltaire, Colonsay; 103, Loch an Eilein, Loch Bhasapoll and Loch a' Phuill, Tiree, Lochan a' Chuirn, Loch Ballyhaugh and Loch a' Mhill Aird, Coll; 104, Lochs Papadil and Fiachanis, Rhum; 110, lochan on Scarp, Loch Cistavat, Harris, Lochs Grogary, Scarie and Magarlan, North Uist, almost all the lochans on Berneray and Baleshare, the whole of the machair transition lochs and Lochs Olivat and Dun Murchaidh on Benbecula, all the similar lochs, with Loch Ceann a' Bagh, Lower Loch Ollay, and the stream linking these two, on South Uist, Loch St. Clair, Barra, and Loch na Cuilce, Sandray.

pH Values of Typical Habitats.—Loch a' Mhill Aird, Coll, 5·3–5·5; Loch Olivat, Benbecula, 5·7; Loch St. Clair, Barra, 6·3–6·7; Loch Papadil, Rhum, 6·4; Loch Ballyhaugh, Coll, 6·8; Loch Hallan, S. Uist, 7; Loch na Liana Moire, S. Uist, 7·1; Loch Ardvule, S. Uist, 7·75; Loch Ceann a' Bagh, S. Uist, 7·56; Loch Bornish, S. Uist, 6·6.

As usual, *P. gramineus* was placed in the pond at home, but few observations were made. It began to produce leaves on 27th February, after which it was destroyed by the pond snail, *Limnaea stagnalis*.

Although its habitats exhibit a pH range of 5·3–7·75, it shows a clear preference for lochs on the machair in which the pH values lie around the neutrality level; so obvious was this that we ceased to search for it in other localities and were, in consequence, greatly surprised to see it in such lochs as Loch Mhor on Scarp and Loch a' Mhill Aird on Coll.

Whilst *P. gramineus* may grow alone, as in an angle of Loch Scarie, N. Uist, or with one companion as in the stream linking Loch Ollay with Loch Ceann a' Bagh, where it struggles with *P. natans*, it is a very social species. In Loch Altabrug, S. Uist, the first station known to us, we listed with it *P. filiformis*, *Caltha palustris*, *Littorella uniflora*, *Myriophyllum spicatum*, *Scirpus lacustris*, *Equisetum limosum* and *Chara vulgaris*, whilst a few miles away, in Lower Loch Ollay, it flourishes with *Lobelia Dortmanna*, *Littorella uniflora*, *Scirpus fluitans*, *P. pectinatus* (rare), *P. natans*, *P. polygonifolius*, *P. Millardii* and *Naias flexilis*.

A glance at lists given in our discussions of other species will provide additional examples of associations favoured by it; in particular, under the heading of *P. natans*, there will be found a list for Loch a' Mhill Aird, Coll, where it meets very strange companions.

× **Potamogeton sparganifolius** Laestad. Ap. Fries (= **P. gramineus** × **P. natans**)

Here we take up another rare hybrid discovered by us in the Outer Hebrides in 1940 in Loch na Liana Moire. When we first collected it, it had been recorded for few British stations; now the known localities have increased in numbers. Moreover, we ourselves have recognized it in Loch Cistavat, South Harris, a further Hebridean station.

In Loch na Liana Moire it covers considerable areas, sometimes alone and sometimes in association with × *P. Billupsii*, and with both or either of its parents. However, in 1947, in one respect, circumstances appeared different from what they were in 1940, for, whilst *P. gramineus* has not disappeared, it is now represented by poorly developed plants very difficult to detect; in 1947, therefore, *P. sparganifolius* was never observed in close proximity to *P. gramineus*. Occasionally, when it grows independently, as in the south-western fringes of the loch, it shows very luxuriant development.

One noteworthy fact about × *P. sparganifolius* in Loch na Liana Moire lies in the circumstance that it never flowers. Like × *P. Billupsii* it spreads vegetatively by means of its creeping subterranean stems, with its vigour enhanced by inherent heterosis depending upon its hybrid origin. In spite of this, it seems certain, judging from the distribution of the plant in the loch, that the population has originated in more than one act of interspecific hybridity.

Compared with Maam, Co. Galway, examples, those from Benbecula are much more delicate, with the differentiation between the upper and the lower leaves much less obvious, and the former tending to become linear. In our opinion, the superior robustness of the Irish examples lies in the fact that they grow in fairly deep running water, whilst ours have developed in a shallow and placid loch. Loch Cistavat plants, growing under conditions parallel to those in Loch na Liana Moire, agree closely with those from the latter station.

Potamogeton alpinus Balb.

In *P. alpinus* we come to a species not only of sporadic occurrence in the Hebrides, but also poor in individuals where it does appear. Our first acquaintance with it was made in 1937, when Dr. K. B. Blackburn collected it in a lochan on the isle of Rhum (v.-c. 104), where it grew with *Nymphaea alba*, *Littorella uniflora*, *Myriophyllum spicatum*, *Lobelia Dortmanna*, *Sparganium angustifolium* and *P. polygonifolius*. This remained the sole station known to us until 1940, when in August we dredged it sparingly from lochans near Nunton and Oban Uaine, Benbecula (v.-c. 110). Later in the same year, in September, J. Heslop Harrison discovered it in quantities in Colonsay (v.-c. 102), where he found it associated with *P. perfoliatus*, *P. gramineus* and *P. pusillus* in Loch Fada, as well as in the Glen Burn, with much the same set of companions reinforced by *P. polygonifolius*. Six years later, in 1946, Dr. W. A. Clark collected the finest Hebridean specimens we have ever examined in a loch near Daliburgh, S. Uist (v.-c. 110), where the pH value was 7·1.

However, one other locality in the Outer Isles has been recorded, as Dr. E. A. T. Nicol reported it from the brackish Loch Leodasay, North Uist; the pH values in that loch in 1935 ranged from 8·3 to 9·4. She mentions that it grows sparingly with *Sparganium angustifolium* in deeper waters, and that the other vascular plants growing in the shallower water were *Lobelia Dortmanna*, *Myriophyllum alternifolium*, *Potamogeton natans* and *Chara delicatula*.

× **Potamogeton prussicus** Hagstr. (= **P. alpinus** × **P. perfoliatus**)

Until collected by us in 1940, this hybrid was unknown in the British Isles, and recognized only in a few lakes in Germany and Norway.

We discovered it in three localities, two in Colonsay (v.-c. 102), and one in Benbecula (v.-c. 110). In the former island, it occurred in the Glen Burn, near Kiloran, and in Loch Fada, and in Benbecula in a lochan between Craigastrome and Oban Uaine, in all cases in a mixed association with *P. alpinus.* From the latter circumstance, it will be clear that it bore a considerable resemblance to *P. alpinus*, of which it was at first deemed to be an aberrant form. Even when dried specimens were subjected to critical examination, although it attracted attention by the deep green coloration of its leaves and other peculiarities, it was still referred to that species. Eventually, however, attaching special weight to its semi-amplexicaul leaves, the condition of its ligules and to its associated plants, we determined it as being a new hybrid with the parentage *P. alpinus* × *P. perfoliatus*, and as such described as new under the name ×*Potamogeton Johannis* in *Occasional Notes from the Department of Botany, King's College, Newcastle upon Tyne*, No. 2, April 1941. In regarding it as new, however, we were mistaken, for, after studying Hagström's *Critical Researches*, we learnt that he had described it already as ×*P. prussicus.* Nevertheless, the determination of the parentage of these Hebridean plants, and the introduction of the hybrid to British lists, result solely from our labours.

Potamogeton perfoliatus L.

In *P. perfoliatus* we again encounter one of the more widely distributed species of pond-weed, for it grows in the whole of the four vice-counties we are considering.

Localities.—v.-c. 102, Loch Fada and other lochs, Colonsay; 103, Loch Bhasapol and Loch an Eilein, Tiree, Loch Cliad, Coll; 104, many lochs on Raasay, Storr lochs, Skye, Lochs Papadil, Dornabec, Fiachanis and the Long Loch, Rhum; 110, lochans on Scarp, Lochs Grogary, Scarie, Magarlan and Skealtar, North Uist, lochans on Berneray, Baleshare and Grimsay, Lochs Olivat and Dun Mhurchaidh, Benbecula; all the machair lochs, with Lochs Snigisclett and Lower Loch Ollay on the moorlands, on South Uist, Lochs Uisge, St. Clair and Doirlinn, with a lochan near Loch Obe, on Barra. In the latter station it occurred as a very large-leaved form which may form the basis of certain Barra records of *P. praelongus.*

pH Values of Typical Habitats.—Loch Cliad, Coll, 5·4; lochan on Grimsay, 5·6; Loch Olivat, Benbecula, 5·7; Loch Doirlinn, Barra, 5·7; Loch Papadil, Rhum, 6·4; Loch Bornish, 6·6, and Loch Altabrug, 7·13, S. Uist; Loch Eadar da Bhaile, Raasay, 7·2.

Of pond-weeds, *P. perfoliatus* is one of the most variable, and, therefore, to test the results of environmental changes, plants were removed to the pond at home in 1944. After wintering safely, these commenced to grow again early in February 1945. On the 18th of that month pale-coloured shoots about two inches long were observed, which gave rise to green leaves on 3rd March. Then, as happened in the case of *P. gramineus*, the pond snail *Limnaea stagnalis* destroyed the plants.

Under natural conditions, *P. perfoliatus* seems much more tolerant of a lower pH medium than any other Potamogeton studied except *P. natans* and *P. polygonifolius*. Thus it is the first associate one finds with *P. natans* as more strictly acid moorland waters are left behind, and it is speedily joined by *P. gramineus* as the machair is approached. Typical of its moorland habitats is the lochan on Grimsay, where its associates were *Myriophyllum spicatum*, *Littorella uniflora*, *Lobelia Dortmanna*, *Scirpus fluitans*, *P. natans* and *Isoetes lacustris*. Loch Olivat yielded much the same plants with the species increased by *Menyanthes trifoliata*, *Utricularia minor*, *Myriophyllum alterniflorum*, *Potamogeton gramineus* and *Carex rostrata*. Loch Dun Mhurchaidh represents another phase, with the assemblage of plants including *Ranunculus trichophyllus*, *Myriophyllum spicatum*, *Hippuris vulgaris*, *Callitriche intermedia*, *Elatine hexandra*, *Apium inundatum*, *Scirpus fluitans*, *P. Millardii*, *P. gramineus*, ×*P. nitens*, *Zannichellia palustris*, *Naias flexilis*, *Eleocharis palustris* and *Equisetum limosum*.

Very different is the picture presented by the Long Loch, Rhum. There one would assume that the vegetation consisted in the main of *Myriophyllum spicatum*, *Littorella uniflora*, *Scirpus fluitans*, *Isoetes lacustris* and a very little *P. natans* and *Phragmites communis*; yet proceeding from very great depths in the centre of the loch, to push their flowering spikes above the surface of the water, are *P. perfoliatus* and *P. praelongus*.

×**Potamogeton nitens** Weber (= **P. gramineus** × **P. perfoliatus**)

This hybrid may be regarded as one of the most plentiful in the Hebrides, for crossings between the two parent species take place with extreme facility. In Colonsay (v.-c. 102) it occurs in Loch Fada and Loch Sgoltaire; in Tiree and Coll (v.-c. 103) in Loch an Eilein and Ballyhaugh Loch; in Rhum (v.-c. 104) in Loch Papadil; in the Outer Hebrides (v.-c. 110) in Little Loch Borve, Berneray, Lochs Grogary and Scarie, North Uist, Loch Mhor, Baleshare, Loch Dun Mhurchaidh, Benbecula, and in many lochs from Loch Ollay to Loch Hallan, South Uist.

The variation of ×*P. nitens* seems kaleidoscopic in its nature. Part of this depends upon the plastic nature of *P. perfoliatus*, a species shown experimentally in a masterly fashion by the two Pearsalls to respond readily to changes in light intensity. Besides, observation shows that the nature of the substrate and the pH values of the water have their influence upon both parents and hybrid. Further, although we have yet to discover ×*P. nitens* bearing perfect fruit, we feel confident that back crosses between it and its parents do arise. Thus ×*P. nitens* populations may include mixed assemblages of F_1 and later generations, intermingled with back crosses of varying types. To put it plainly, segregates may be present genotypically and phenotypically making a complete bridge between *P. gramineus* and *P. perfoliatus*. This bridge, in view of the fact that *P. gramineus* and *P. perfoliatus* belong to relatively widely separated subsections of the genus, would in itself account for much of the variation observed.

×**Potamogeton Heslop-Harrisonii** Clark (= ×**P. nitens** × **P. Millardii**)

This rather extraordinary plant was collected in Loch Grogary, North Uist (v.-c. 110). From my first examinations I came to the conclusion that its parentage was *P. gramineus* × *P. Millardii*. Dr. Clark, however, after making a series of painstaking anatomical and other studies of the plant, put forward the view that it had the parentage stated above.

However, now that it is recognized that *P. alpinus* possesses a much more extensive distribution in the Outer Hebrides than was originally supposed, in my opinion, the parentage *P. alpinus* × *P. Millardii* is not excluded.

Potamogeton praelongus Wulf.

In the Hebrides, *P. praelongus* can only be considered, as far as our observations go, as extremely rare. It came first under observation in Raasay (v.-c. 104) in 1935, in Loch na Meilich (pH 7·3), one of the few Raasay lochs overlying Jurassic rocks. There it was actually seen growing, for it was dredged from a boat. In 1938 it turned up in the Outer Isles (v.-c. 110), when it was picked out of débris on the shores of Loch Kearsinish, South Uist, and, finally, it was detected in the Long Loch, isle of Rhum (v.-c. 104). In both of the stations in v.-c. 104 it occurred in very deep water, in Loch na Meilich mixed with *P. lucens*, and in the Long Loch almost in pure stand, although part of the colony showed an admixture with *P. perfoliatus*. It is very possible that it grows in many other deep lochs which, in the absence of a boat, cannot be examined.

Potamogeton epihydrus Rafinesque

In August 1943 there occurred in the north-east angle of Loch Ceann a' Bagh (pH 7·52) a very puzzling Potamogeton. In many respects the plant bore the general aspect of a hybrid of *P. gramineus*; in particular, in its apparently sterile inflorescence, the fewness of the floating leaves and their occasional absence, it strongly recalled ×*P. Billupsii* (=*P. coloratus*×*P. gramineus*). The submersed leaves, however, in their lengths, breadths and parallel sides proved difficult of interpretation unless these features were due to the influence of *P. polygonifolius*. This led to the tentative determination of the plant as ×*P. Seemenii* Asch. and Gr., a plant of the parentage *P. polygonifolius*×*P. gramineus*. Against this were the build of the submerged leaves and their neuration. Temporarily, the matter was shelved by regarding the plant as a strange form of *P. polygonifolius*.

In 1944, however, the acumen of Dr. W. A. Clark led to the discovery of another strange plant in a lochan slightly to the north of Loch Ceann a' Bagh, which, from a consideration of its submersed leaves, I had no hesitation in determining as the American species *Potamogeton epihydrus* Raf. This plant, Dr. Clark, as its discoverer, will no doubt discuss fully in a future paper.

In examining Dr. Clark's plants I was strongly impressed by the cellular-reticulate appearance of those portions of the leaf blades lying within the inner nerves of the submerged leaves. Making comparisons with my own material, it was apparent at once that my plants bore some relationship to those of Dr. Clark. In fact, for some time I considered them to be ×*P. concilius* Ar. Benn. (=*P. epihydrus*×*P. gramineus*).

Further study, however, made it clear that they represented a younger and submerged state of the plant to which Fernald applies the name *P. epihydrus* Raf. var. *Nuttallii* (Cham. & Schlecht).

The strong development of the lacunae in the submersed leaves, and the delicate texture, length and breadth of the same leaves, are features leading to the easy recognition of the plant.

Potamogeton Friesii Rupr.

Up to the present, only in the Outer Isles (v.-c. 110) have Hebridean stations been shown to exist for *P. Friesii*; there the plant occurs in three isolated localities: one in Loch Mhor on the isle of Baleshare, a second in a drainage channel flowing northward near Loch Kildonan, South Uist, and a third in Loch St. Clair, Barra (pH 6·3–6·7). In the first and third of these stations it is distinctly rare, but in the second it occurs in dense, well-grown masses, practically free from admixture with other plants except a little *Myriophyllum spicatum.* In the southern stretches of the lode it yields place to *P. natans.* In this station its appearance offers a great contrast to the plants found in Loch Mhor, for the latter are very delicate in texture. Indeed, so interesting did the Baleshare plant appear, when critically examined, that a journey was made to the loch in August 1947 to study it and another speciality, *P. rutilus.* However, all our hopes were frustrated, inasmuch as the whole of the Baleshare lochans had been rendered unworkable by the enormous algal growths developed in them as a result of the protracted drought.

Kept under observation in the pond, plants removed from their natural habitat began to grow after their winter rest in the middle of February. On the other hand, winter buds which had lain on the bottom throughout late autumn and winter began to root on 11th March, after which both lots of plants made rapid progress and began to flower on 27th June. A little later, on 8th July, the first winter buds of the year were cast, and the process continued for quite a considerable time.

It was very curious to note the difference between the attitude adopted by the pond snail, *Limnaea stagnalis,* towards *P. Friesii* and that displayed in the case of *P. perfoliatus* and *P. gramineus.* The latter two were eaten voraciously, whilst *P. Friesii* was entirely neglected.

Potamogeton rutilus Wolfg.

This very rare pond-weed was collected in 1942 in Lochs Scarie and Grogary, North Uist, by Dr. Clark and myself, and in Loch Mhor, in the adjacent isle of Baleshare, by myself; these gatherings formed the basis of the first record for v.-c. 110. Previously to our discovery, the species had only been recognized, so far as the British Isles were concerned, in the Shetland Islands. When we examined Lochs Scarie and Grogary, enormous quantities of débris lay on their shores as a result of a succession of south-westerly gales. The tangle in the case of Loch Grogary proved exceedingly productive, for it yielded *Myriophyllum spicatum, Callitriche intermedia, Pota-*

mogeton natans, *P. gramineus*, *P. perfoliatus*, × *P. nitens*, *P. rutilus*, *P. pusillus*, *P. Millardii*, *P. pectinatus* and *Naias flexilis*.

A careful study of these specimens has been made, and they have been fully discussed in the *Proc. Univ. Durh. Phil. Soc.*, x, 368–373, 1943, but it seems necessary to point out that the North Uist plants were of a much stronger type than those from Baleshare, although in both cases the characteristic winter buds were such as to render any mistake in identification quite impossible.

Examination of Lochs Grogary and Scarie could not be carried out this year, but Loch Mhor, Baleshare, was visited with a view to our extending our studies of its rarities: for reasons already stated, these ended in complete failure.

Potamogeton pusillus L.

In the past, this species has been confused with *P. Millardii*, with the consequence that many early records are quite unreliable. Curiously enough, under natural conditions, when they are seen growing in the water they are readily differentiated, so striking are their characteristic appearances and habit. It is only when they are studied as dried specimens that real difficulties are experienced in separating them. However, thanks to the labours of Hagström and Fernald, structural features, enabling a diagnosis to be made with complete certainty, are now available; these lie in the open stipular sheaths of *P. Millardii* and the tubular sheaths in *P. pusillus*. Besides these, the winter buds and their disposition are equally diagnostic. In the Hebrides the species is of irregular occurrence, and is easily overlooked.

Localities.—v.-c. 102, Loch Fada and other lochs, Colonsay; 103, stream near Loch Bhasapol, Tiree; 104, Loch Papadil, Rhum; 110, lochan on the isle of Scarp, Loch Grogary, N. Uist, Loch Dun Mhurchaidh, Benbecula, Loch Altabrug to Loch Hallan, S. Uist.

pH Values of Typical Habitats.—Loch Kildonan, S. Uist, 6·8; pool, 6·2; Loch Papadil, 6·4; clay-pit, 6·7; Loch Hallan, S. Uist, 7.

For the most part, we have obtained this species in the "wash" driven ashore by strong winds, and from that fact we deduce that *P. pusillus* is very often an inhabitant of fairly deep waters. Still, we have observed it growing at depths varying from a few inches to two feet. In Loch Papadil, isle of Rhum, where it occupied sandy mud in about six inches of water, it was surrounded by masses of *P. natans*, *P. gramineus* and *P. perfoliatus*, but in its own area its companions were *P. filiformis*, *Elatine hexandra*, *Scirpus fluitans* and

Chara delicatula. At another point, associated with it were *Ranunculus sceleratus*, *Juncus bulbosus*, *Eleocharis palustris*, *P. polygonifolius*, *Lemna minor* and *Glyceria fluitans*. On Tiree the only plants growing with it were *P. filiformis* and *Scirpus fluitans*, whilst in Lochs Hallan and Kildonan it can be found in every possible combination of the plants proper to a machair loch.

P. pusillus, even in its favoured localities, is very erratic in appearance from year to year. Thus, in 1939, in one locality in which it was discovered it abounded, and, moreover, fruited freely. Notwithstanding this, in the following year its numbers fell off in that station, although masses of it grew in another pool not far away. Now it has quite vanished from its original habitat.

These fluctuations, in my opinion, depend upon the degree of freedom of movement of the winter buds. When the water is low, or when other circumstances, like the presence of a dense bank of *Lemna minor* and its débris, check such movement, then, in the ensuing season, *P. pusillus* becomes exceedingly scarce.

Potamogeton Millardii Heslop Harrison (=**P. Berchtoldii** Dandy and Taylor non Fieber)

This is another widely spread Hebridean pond-weed with a distribution probably greater than that now on record.

Localities.—v.-c. 102, West Loch Fada, Colonsay; 103, Loch Ballyhaugh, Lochan a' Chuirn and a lochan near Loch a' Mhill Aird, Coll, Loch a' Phuill and its exit stream, Tiree; 104, Loch Papadil, Rhum; 110, Loch Mhor, Scarp, Little Loch Borve, Berneray, Loch Grogary, N. Uist, Loch Mhor, Baleshare, Loch Dun Mhurchaidh and many western lochs, Benbecula, Howmore to Loch Hallan, S. Uist, Loch nam Faoileann, Barra. The subspecies *lacustris* Pearsall and Pearsall f., a very well characterized and beautiful form, has been collected in Loch Fiachanis, Rhum and Loch Snigisclett, on the eastern moorlands of S. Uist.

pH Values of Typical Habitats.—Loch nam Faoileann, Barra, 5·6; clay-pit, 6·2; Loch Ballyhaugh (east), Coll, 6·3; Loch Papadil, Rhum, 6·4; Loch Hallan, S. Uist, 7.

Depending, no doubt, upon local circumstances governing its distribution, this pond-weed may often be seen growing in enormous masses close in shore. Normally, in such instances, it possesses no associates. Occasionally, however, small infiltrations are made into its ranks by *Myriophyllum spicatum*. On one occasion, in a small sheet of water, except for algae, its sole companion was *P.*

crispus, and both species abounded. In Loch nam Faoileann, Barra, its associates are increased, but still remain scanty; they are *Littorella uniflora*, *Sparganium angustifolium*, *P. natans*, *Eleocharis palustris* and *Equisetum limosum*. On South Uist, and elsewhere in the machair and machair-moorland transition lochs, it may be included in all of the associations listed for such waters, but in Loch Snigisclett it is accompanied by much the same plants as in the Barra station, with the addition of *Isoetes lacustris*.

P. Millardii, as far as our experience goes, flowers but rarely, and in the absence of an interlacing system of subterranean stems it seems to depend upon its winter buds for reproduction and dispersal. As a result, like *P. pusillus*, it is very capricious in appearance and abundance. In one locality, examined in 1945, it existed as a dozen scattered plants; in 1946 it had vanished. This year it forms a broad dense band along a fifty-yard stretch of the water edge. Undoubtedly, the prevalent winds had favoured the massing of drifting winter buds there in the autumn of 1946 from some point in deeper water, not observed in that season.

Plants placed in the pond in 1943 commenced to cast their winter buds immediately, and the process continued for several weeks. The buds lay dormant until late February 1944, when activity recommenced, so that on 2nd March most of the buds were already rooting, and a few precocious individuals exhibited short, broadish leaves. Growth proceeded steadily until 31st May, when the plants had reached the surface of the water and were bushing out. In spite of the apparent suitability of their habitat, and their luxuriant growth, none flowered, and winter buds were seen floating in the last week of August. It seems important to note that, in almost dried-up pools half a mile away, *P. Millardii* was fruiting freely; clearly, there is a distinct connection between the depth of water and the successful flowering and fruiting of the species.

Potamogeton crispus L.

Although *P. crispus* is on record for v.-cs. 102 and 104, we have not seen it in those vice-counties; nor have we seen it in Coll and Tiree. In the Outer Isles, on the other hand, we have detected it in a number of stations, but, even there, its distribution is very erratic. If we may be permitted to employ such a statement, its headquarters seem to be on North Uist, where it is locally common in machair lochs and streams; amongst its localities in that island are Loch Sandray, a lochan near Bayhead, a runnel on the Clachan

Sands, and a stream draining Loch Hosta. Toward the north, it was collected on the isle of Berneray, Sound of Harris, in Loch Bhruist and Little Loch Borve; whilst to the west it is not uncommon in lochans on the isle of Baleshare. Southward it thins out, for it fails on Benbecula, and has been noted only on South Uist in Loch a' Mhachair and in a lochan close to Ormaclett.

This year, when we visited the lochan near the school on Baleshare, a station in which it was doing well in 1942, it was again observed. Clearly, however, it was utterly unable to maintain itself against the pressure of huge masses of algae; it only persisted as attenuated weaklings, quite unable to flower. In fact, the only plants capable of holding their own were *P. pectinatus*, *Myriophyllum spicatum* and a little *Ranunculus trichophyllus*. In the lochan at Ormaclett its companions were *Polygonum amphibium*, *Littorella uniflora*, *Myriophyllum spicatum*, *P. gramineus*, *P. perfoliatus* and *P. natans*.

In many of its habitats it exhibited an unmistakable predilection for swiftly running waters, and seemed to thrive in them without associates; nevertheless, it was quite obviously satisfied with the stiller and deeper waters of the machair lochs in the presence of various combinations of associates.

P. crispus not only fruits well but, in addition, hibernates by means of its underground rhizome system, which provides it with a method of conquering new territory. Superimposed upon this, too, is the prolific production of its peculiar winter buds which assist in its vegetative reproduction and dispersal. As these winter buds are torn off and scattered far and wide by water-fowl, it is difficult to understand why, in the presence of innumerable mallard, swans, etc., the areas occupied by the plant are not increased greatly in the Outer Isles, both generally and in individual lochs.

In my observation pond, throughout the winter of 1943–44, the rhizomes seemed to make slight growth, so that on 3rd March 1944 the young shoots were already three inches long. Moreover, the detached, but developing, winter buds were already well rooted then. Still, progress was far from rapid, for the plants were only fully provided with leaves on 31st May and began to flower on 24th June. Quite unexpectedly, winter buds began to leave the parent plants on 20th July, and the process continued for several weeks.

× **Potamogeton Cooperi** (Fryer) Fryer (= **P. crispus** × **P. perfoliatus**)

This hybrid was collected with the parents in the Ormaclett Castle locality on S. Uist. Plants removed to an aquarium flourished well, but failed to flower. They did, however, form and cast winter buds of a strange and reduced structure.

Subgenus **Coleogeton.**
Potamogeton filiformis Pers.

In the Hebrides this species may, at best, be described as locally plentiful.

Localities.—v.-c. 102, in several lochs, Colonsay; 103, splash-pool near Calgary Point, Coll, splash-pools between An Cnap and Rudh' an Fhaing, runnel near Cornaigmore, An Fhaodail, and in the western lochs, Tiree; 104, lochs on Raasay, Lochs Papadil, Fiachanis and Dornabec, Rhum; in nearly every machair loch in Berneray, Benbecula, S. Uist and Barra.

pH Values of Typical Habitats.—Loch St. Clair, Barra, 6·7; Loch Hallan, S. Uist, 7; Loch na Liana Moire, Benbecula, 6·9–7·1; Loch Papadil, Rhum, 6·4; splash-pools, Coll and Tiree, 7·5–7·9.

Judging from its numerous stations in the Hebrides, it seems to prefer the sandy edges of lochs, where it often forms a marginal fringe extending from the shore to depths of two feet. In such areas, its rhizome creeps far and wide, thereby often developing an extensive mat. *Potamogeton filiformis* commences to grow very early in the season. Under semi-natural conditions, Benbecula plants, removed from Loch na Liana Moire in 1944, began to show elongation of their rhizomes during the first week in March 1945, with the result that on 17th March the first tuft of leaves was almost six inches high, whilst that nearest the growing point was just short of two inches. This precocity in growth must likewise characterize the plant in nature, for in Coll and Tiree splash-pools, as well as in Lochs Hallan and Bornish in South Uist, the species comes into flower in May and early June.

Flowering and fruiting proceed smoothly at all depths from four to twenty-four inches. Even in the deeper splash-pool at Calgary Point, Coll, where the elongated plants may attain a maximum height of nearly three feet, these operations are equally successful. The fruits ripen in September, but remain in a green state on the plants under water for a very long time; finally, they fall and sink to the bottom. Curiously enough, just prior to germination, many fruits come to the top of the water for a short time, only to sink finally. This, of course, aids the dispersal of the seeds. Kept in an aquarium under artificial conditions, Benbecula fruits, although frozen solid more than once, commenced to germinate on 5th

February. After a check, by further frost, the process recommenced on 26th March, and continued at irregular intervals for several weeks.

Although, as is often the case in splash-pools and pans in salt-marshes, *P. filiformis* may possess but few or no companions, it normally, as the outcome of its usual favourable environmental conditions, has a selection of associated species which varies but little in composition from habitat to habitat. In Loch Bornish, for example, there grow on the same sand-belt the following species: *Myriophyllum spicatum*, *Hippuris vulgaris*, *Littorella uniflora*, *Polygonum amphibium*, *Scirpus fluitans*, *S. lacustris*, *S. maritima*, *Eleocharis palustris*, *Potamogeton pectinatus*, ×*P. suecicus*, *P. gramineus*, *P. perfoliatus*, *P. natans*, *Equisetum limosum* and *Chara hispida*. In this association *P. filiformis* tends to approach much nearer the shore than *P. pectinatus*, whilst *Eleocharis palustris* often forms "islands" within the zone in which *P. filiformis* reaches its maximum concentration.

If we proceed northward or southward from Loch Bornish to other lochs, odd species may drop out, in particular *Scirpus lacustris* and *S. maritima*, but, on the whole, the assemblage shows but little change.

Potamogeton pectinatus L.

Localities.—v.-c. 102, lochans in the north-west of Colonsay; 103, Lochs Stanail, a' Phuill and Bhasapol, Tiree; 104, several lochs on Raasay, Lochs Dornabec, Papadil and Fiachanis, Rhum; 110, Little Loch Borve, Berneray, Loch an Duin and other brackish lochs, N. Uist, Loch Mhor and lochans on Baleshare, Loch Sniogravat, Monach Isles, Loch Torcusay, Loch na Liana Moire, Loch Mhor, etc., Benbecula, the brackish Lochs Bee and Ceann a' Bagh, and the machair lochs from Loch Roag to Loch Hallan, S. Uist, Lochs St. Clair and an Ail, stream near Eoligarry, Barra.

pH Values of Typical Habitats.—Loch Chadhacharnaich, Raasay, 8·2; Loch an Duin, N. Uist, 8·8; Loch Ceann a' Bagh, S. Uist, 7·52; Loch na Liana Moire, S. Uist, 7·1; Loch Ardvule, S. Uist, 7·59; Loch Bornish, S. Uist, 6·6.

As will be perceived from a glance at the figures shown above, *P. pectinatus* can tolerate environments of pH 6·6 to well above neutrality. These values it finds in lochs in the machair-moorland transition zones, on the machair and in brackish waters. It is, in fact, the only Potamogeton really to flourish in the latter type of habitat.

P. pectinatus, like its ally *P. filiformis*, often grows without associates, this preference being very noticeable in the cases of pans in salt-marshes. More frequently, however, in such situations, it has one companion, generally *Zannichellia maritima*, although at times, even in adjoining pans, that may be supplemented by *Myriophyllum alterniflorum* and *Enteromorpha intestinalis*. In the Hebrides, whilst it is sometimes found in runnels only a few inches deep, pure colonies are often formed in lochs at considerable depths. Thus, on Benbecula, in Loch Torcusay, it occurs from the centre right up to the shore, as well as in the tiny stream linking that loch with Loch na Liana Moire. In the latter loch it avoids the shore and rarely associates with other plants. Instead, it occupies large areas of deep water lying within the *P. natans* zone, where it develops dense masses, practically pure in composition, except for a slight admixture with *Chara hispida* on the fringes. In really brackish lochs like Loch an Duin, North Uist, in which the plant occupies the areas most remote from the open sea, it grows alone in the deeper portions with the greater salt content, but elsewhere, in the fresher tracts, are associated with it *Myriophyllum alterniflorum* and *Ruppia rostellata*. Again, in Loch Ceann a' Bagh, South Uist, also more or less subjected to tidal influence, its only associates are a little *Littorella uniflora*, *Myriophyllum alterniflorum*, *Fucus vesiculosus* and *Enteromorpha intestinalis*; there it is established in that stretch of the loch at the head of Loch Eynort--a long narrow sea-loch. In Loch Ardvule, at times liable to an influx of the sea, it mixes with the following associates: *Myriophyllum spicatum*, *Hippuris vulgaris*, *Ranunculus Baudotii* var. *marinus*, *Polygonum amphibium*, *Littorella uniflora*, *Iris pseudacorus*, *Scirpus maritimus*, *Eleocharis palustris*, *Lemna minor* and *Phragmites communis*. Other associations including *P. pectinatus* are listed in connection with other species.

Like *P. filiformis*, *P. pectinatus* increases readily by means of tubers and creeping subterranean stems, but its seasonal growth commences much later than in the case of its ally. Thus on 10th April 1945, when *P. filiformis* had already made considerable progress, only the white tips of its rhizomes were visible above the soil at the bottom of the water. However early in May, at the depth of three feet, shoots four inches long were observed, and the earliest of these reached the surface on 23rd May. Subsequently they branched out far and wide over the water, and came into flower on 1st July. By 12th September the fruits had ripened, and many were floating about quite freely. Amongst these, when a collection was made on 8th October, were found numbers of tiny tubers. On the same date, practically the whole of the stems and foliage had broken up, so that a week later no traces of them could be seen. From a consideration of these facts, it will be obvious that *P. pectinatus* passes through its reproductive stages much more speedily than *P. filiformis*.

Perhaps this is a proper point to insert one or two rather noteworthy observations. In warmer Hebridean lochs the green shoots of one year often persist until late in the following season. In Loch Hallan, for instance, in 1942, growth made in 1941 was still fresh and green in June. Again in 1945, when water-levels in many lakes sank markedly in early September, heavy rain fell after *P. pectinatus* had died back. Almost immediately the plants sent forth new growths, until the new water-level was reached; then they flowered for a second time. Further, it should be noted that, if at any time during the growing season the water-level changes temporarily, then the plants readjust themselves quite readily to such changed conditions.

The fruits and tubers collected on 8th October 1945 were placed at once in an aquarium, but it was not until 3rd January 1946 that any signs of germination were perceived; then five seeds had germinated. At the same time, the little tubers were likewise thrusting forth shoots. Soon after, frost came, and fruits and tubers alike were frozen solid. After the ice disappeared the young *P. pectinatus* plants were quite healthy, and soon renewed their growth, one seedling in particular showing excessive vigour. A few days later a very few additional seeds began to move, but the majority remained dormant until 30th August when further seedlings were noted in the tank. These, however, proved to be the last of the year.

× **Potamogeton suecicus** Richt. (**P. filiformis × P. pectinatus**)

So far, we have only detected this hybrid in the Outer Isles (v.-c. 110) and in Tiree (v.-c. 103). Naturally enough, one would anticipate its occurrence solely in localities in which its parents met, and that for the most part truly represents the position as in Little Loch Borve, Berneray, Loch na Liana Moire, and lochans near Gramisdale and Borve Castle, Benbecula; Loch Bornish and Loch Hallan, S. Uist. Yet in the Baleshare habitats only one parent, *P. pectinatus*, seems to occur; there, further attempts to demonstrate the presence of *P. filiformis*, made in 1947, were baffled by profusion of algae in the lochans.

Furthermore, in the only Tiree station known to me, a stream flowing from Loch a' Phuill into Balephuil Bay, the only other Potamogeton present is *P. natans*, and a close inspection of the colony this season (1947) only served to confirm our original observations. In that station the plant forms dense masses for considerable stretches of the stream. For this abundance two causes may be assigned: (1) the direct effects of heterosis (or hybrid vigor) and (2) the exceedingly great energy with which vegetative reproduction, amplified by the heterosis, takes place.

× *P. suecicus*, in the Hebrides, seem more or less sterile; still it does produce, at rare intervals, some functional pollen, as well as occasional fruits. Thus the stage is set for the development of an F_2 lot and back crosses. These circumstances alone would account for much of the huge range of variation exhibited by the hybrid; almost certainly, the major part of the remainder depends upon environmental influences of various types.

Our best thanks are due to King's College (University of Durham) Research Committee for their generous contributions to the expenses of our expeditions.

Addendum.

Additional records for 1948:—

Potamogeton gramineus L.—v.-c. 110, Loch Barvas More, Lewis.

Potamogeton perfoliatus L.—v.-c. 110, Lochs on Lewis from Barvas to Shawbost.

Potamogeton nitens Weber.—v.-c. 110, Loch Barvas More, Lewis.

Potamogeton pectinatus L.—v.-c. 110, Pools west of Coll sands, Lewis.

FIELD STUDIES IN ORCHIS L. I. THE STRUCTURE OF DACTYLORCHID POPULATIONS ON CERTAIN ISLANDS IN THE INNER AND OUTER HEBRIDES. By J. HESLOP HARRISON, M.Sc., Ph.D. (With Pls. I and II.)

(Read 15th April 1948.)

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INTRODUCTION.

The phytogeographical interest of the British Dactylorchids has been considerably enhanced in recent years by the recognition of new forms, certain of which apparently lack continental counterparts, and, further, possess suggestive patterns of distribution even within the British Isles. Among those newly described, *Orchis majalis* Reichb. subsp. *occidentalis* Pugsl. and subsp. *Traunsteinerioides* Pugsl. (Pugsley, 1935, 1936) and *O. kerryensis* Wilm. (Wilmott, 1936) occur in Ireland in or near areas long noted for their possession of plants of anomalous distribution, including those forming the so-called Lusitanian element of the British flora. Even if these Irish orchid species and subspecies prove to be ". . . but variants of one variable species," which is the opinion of P. M. Hall (1937), cautiously expressed after examination of the plants *in situ*, the significant fact remains that that species cannot be matched in England or on the Continent. The discovery of *O. majalis* subsp. *occidentalis* in the Outer Hebrides (Campbell, 1937; J. W. Heslop Harrison, 1941) merely gives fresh emphasis to its distributional pattern, since there again it is becoming clear that a flora exists which differs in its history from that of the mainland.

Unfortunately the data are still inadequate for a comprehensive survey of the distribution of the components of the sub-genus. In part this is the outcome of former taxonomic confusion, itself resulting from that very polymorphism which lends the group its present interest. Apart entirely from the apparent geographical variability, natural colonies generally display within themselves wide variation in many of the characters variously employed as taxonomic criteria. There seem to be few sterility barriers in the sub-genus, and, particularly in areas subject to human interference, hybrid swarms add to the burden of complexity. The case for the utilisation of mass-collection technique in dealing with the group is clear.

The present paper is an attempt to assess the constitution and structure of Dactylorchid populations over a small part of the British range of the sub-genus, that is, in certain islands of the South- and Mid-Ebudes and the Outer Hebrides. Methods of mass collection and biometrical analysis have been adopted, and some ecological data amassed. It has become increasingly clear throughout the study that much of the variation encountered is related to environment, both in delicate adjustments of such plastic factors as plant stature, and in the rather more significant correlation which exists between certain habitat factors, in particular soil-pH, and the occurrence of recognisably distinct subspecies and varieties. Furthermore, even in the small area so far covered there is evidence of slight geographical differentiation in certain species, apparently unrelated to habitat factors. A precedent for the application of biometric methods to the study of "difficult" plant groups and hybrid populations in the field is to be found in the work of Anderson (1936, etc.) on *Iris* and *Tradescantia*, which has been followed by various workers in America and Europe. Elaboration of the technique, with further refinement in the use of large cultures grown under controlled conditions in experimental gardens, is an important tool in genecological studies of the type initiated by Turesson: noteworthy examples may be found in the work of Gregor's school on *Plantago* (1936, 1938), and in the extensive researches, ecological, systematic, and cytological, of Clausen, Keck, and Hiesey at Stanford (1940). Nevertheless, the greater control over living material provided by experimental garden technique in no way detracts from the importance of field studies, for ultimately the study of evolution is the study of events, past and present, "in the field." The methods are, in effect, complementary.

Dactylorchis taxonomy still remains a subject for vigorous debate. Thus it is clear from the recent statements of Messrs. Vermeulen, Pugsley, and Wilmott (1945), that the identity of *Orchis latifolia* L. has still to be established to the satisfaction of Continental and British specialists. Nevertheless, Pugsley's identification of the species with the plant formerly known in this country as "*Orchis incarnata* L." (1935) has met with wide acceptance in Britain and some recognition abroad (*e.g.* by Nevski in the "*Flora* URSS," 1935). The revision proposed by Pugsley is therefore adopted here, and where applicable, his nomenclature is employed for varieties.

Without prejudice to any future decision which may be made relating to the identity of "*Orchis maculata* L.," the term "*maculata* complex" is employed here to designate the group to which the generally recognised species *Orchis Fuchsii* Druce and *O. ericetorum* (Linton) Marshall belong, together with related forms. *O. Fuchsii* (the f. *Meyeri* of Scandinavian workers?) and *O. ericetorum*, syn. *O. elodes* Griseb., probably the variety *genuinus* of certain Continental authors, are clearly distinct morphologically and cytologically, the former a diploid, $2n=40$ and the latter a tetraploid, $2n=80$.

In recognition of the fact that the Hebridean version of *O. Fuchsii* differs slightly in the aggregate from the mainland form, the race was separated as the "species" *O. hebridensis* by Wilmott (1939). Following field and cytological studies, its rank was reduced to that of a variety by J. W. Heslop Harrison (1939). The plant is referred to here as *O. Fuchsii* Druce var. *hebridensis* (Wilmott) Heslop-Harrison.

METHODS.

Orchis species preserve notoriously badly, and frequently lose on drying all trace of those characters which lend them individuality in life. A critical study of natural populations must therefore be a field study in every sense of the word, and biometric data must be garnered from fresh material. However, the choice of suitable characters for biometrical investigation is not a simple one, since if a reasonable area is to be covered within the flowering period, and significantly large samples are to be examined, the methods employed must not be excessively time-consuming; nor must they demand any elaboration in the way of equipment.

The following characters were selected for examination in living specimens:—

Plant stature.
Total number of flowers in the inflorescence (certain cases).
Labellum ground colour.
Lateral sepal markings (certain cases only).
Leaf number.
Intensity of leaf marking.
Stem structure (*i.e.* solid or hollow).

Labellum shape is a key taxonomic feature in the *maculata* complex, and one which demands more careful examination than can normally be afforded in the field. Complete lips were therefore detached from each flower examined, mounted on gummed paper and allowed to dry under slight pressure. By this technique the lip is preserved intact without shrinkage or significant distortion of shape. In the majority of cases a good deal of natural colour is retained, and the patterning of life remains discernible for an indefinite period. Pages of such mounted lips, photographed after a lapse of three months, are shown in Pls. I and II.

The selection of the flower in a particular inflorescence from which to preserve a lip was based upon the considerations set forth in the paragraph on flower colour below. The lips were removed from the living flower with a sharp scalpel, the cut being made exactly at the mouth of the spur, this affording a convenient datum for subsequent measurement.

Sampling Technique.

A preliminary survey of the general distribution of each species in a given island normally sufficed to indicate the undisturbed and uncontaminated colonies, and provided the basis for a selection of more or less circumscribed populations for sampling.

Mass collections were made from each colony so chosen, each consisting normally of a minimum of one hundred individuals. Every care was taken to avoid conscious or unconscious selection for colour, stature, or other factors. The orchids were collected in a series of roughly parallel traverses across the chosen area, and every individual within reach was taken provided that it possessed at least one mature but unwithered flower. It was found necessary to record the statistical data within twenty-four hours of gathering to avoid wilting and loss of flower colour. During examination subsequent to collection, damaged individuals, those with prematurely withered leaves, spikes curtailed by grazing animals, etc., were eliminated. A small percentage of lips failed to preserve after mounting, or were otherwise rendered unsatisfactory for computation of labellum shape index: these have also been rejected.

Plant Stature.

The overall stature of the living plant is not readily ascertained without uprooting, due to the varying depths of the tubers below the soil surface. To avoid the vandalism involved in large scale uprooting, the assessment of height has been based upon the length of that part of the plant which comes free of the soil with a vertical pull at the level of the basal leaves. The stem separates normally just above the tubers, thereby leaving next year's tuber free to develop. Stem lengths are conveniently placed in centimetre classes.

Ecological.

In the case of all the pure populations involved in this study, the habitats are practically natural, and uninfluenced by man except through the agency of grazing animals or in the seasonal cutting of hay. They represent facies of the characteristic plant associations of the Western Isles: duneland, machair,* peat moorland, and the intervening ecotones. Data relating to the typical concomitants of the species have therefore been assembled as likely to provide an accurate guide to their ecological requirements. The frequency of occurrence has been assessed visually, and in Tables I and II the customary frequency symbols have been employed.

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* The term "machair" is applied to the stabilised zone behind mobile duneland. Since the coastal sand accumulations in the Hebrides are generally highly calcareous, the soil-pH in such regions is normally high. Blown dune sand may similarly effect the pH of peat for considerable distances inland from coastal beaches.

Determinations of soil-pH have been made both electrometrically from soil samples and colorimetrically *in situ*. The latter have been made at tuber level, usually at a depth of three to six inches, using Johnson's Universal and Comparator Indicator Papers.

THE POPULATIONS.

The islands covered in the present survey are Tiree, Coll, and Rhum in the Inner Hebrides, and Barra and South Uist in the outer group of islands. All the collation of data relating to *O. Fuchsii*, *O. ericetorum*, *O. latifolia*, and *O. latifolia* var. *coccinea* was done during the early weeks of July 1947. The Rhum form of *O. Fuchsii* was examined in early August 1947, at the peak of its flowering season.

For convenience of reference and comparison, the lists of associated plants in the various localities are brought together in Tables I and II, which follow the population details below.

O. Fuchsii Druce var. **hebridensis** (Wilm.) H.-Harr.

COLL.

Population C. I. Moist hollow in calcareous duneland west of Cliad. The hollow contains a central marsh dominated by *Carex rostrata*, and the orchids abound in a marginal belt some five metres in width in which the dominant vascular species is *Equisetum palustre*. The soil-pH at tuber depth is 6·6. *O. Fuchsii* var. *hebridensis* is the more abundant orchid, and represents 96 per cent. of the individuals present. The remaining 4 per cent. are forms of *O. latifolia.*

Stature: Mean, 25·05 cm.; Standard Deviation, 5·54; Range, 16–37 cm.

Population C. II. Machair edge, between Cliad and Grishipoll. The locality is a lightly grazed meadow, and is fairly representative of the type of ecotone which exists between the machair, characterised by soils of low acidity, and the acid peat moor forming the hinterland. This is a favourite habitat for the present species throughout its Hebridean range, and here it reaches greatest profusion. Soil-pH as follows: 1st plant, 6·0; 25th plant, 5·8; 50th plant, 5·2; 75th plant, 5·5; 100th plant, 5·8—all determined at tuber level. While *O.*

TABLE I.

PLANT LISTS FOR HABITATS OF ORCHIS FUCHSII DRUCE VAR. HEBRIDENSIS (WILMOTT) H.-HARR., O. LATIFOLIA L. SEC. PUGSL., AND O. LATIFOLIA VAR. COCCINEA PUGSL. ON THE ISLANDS OF COLL, TIREE, BARRA, AND SOUTH UIST.

Species.	var. *hebridensis.*					*latifolia.*			var. *coccinea.*	
	C. I.	C. III.	T. II.	T. I.	B. I.	C. V.	C. VI.	B. III.	C. VII.	U. III.
Thalictrum dunense	..	..	..	..	f–la	..	..	..	..	..
Ranunculus Flammula	f	..	f	..	o	f	..	f	f	o
R. acris	o	f	o	o	o	..	..	o	o	..
R. repens	..	..	..	..	o	..	..	..	f	o
Caltha palustris	f	o	..	..	..	f	..	lf	..	..
Cardamine pratensis	o	..	f	..	..	o	..	..	..	..
Viola Riviniana	..	..	..	..	o	..	..	..	..	..
Polygala dubia	..	..	..	..	o	..	..	..	..	..
Lychnis Flos-cuculi	f	lf	..	o	..	f	..	f	..	..
Cerastium vulgatum	..	o	o	..	o	..	..	o	..	..
Arenaria serpyllifolia	..	..	..	..	o	..	..	..	o	o
Sagina nodosa	..	..	..	..	o	..	..	..	o	..
Linum catharticum	..	..	..	..	o	..	..	..	o	o--lf
Trifolium pratense	..	o	..	..	f–la	..	..	o	..	o
T. repens	..	o	..	o	o	..	..	..	lf	f–la
Anthyllis Vulneraria	..	..	..	..	f–la	..	..	o	..	..
Lotus corniculatus	..	o	..	o	lf	..	..	..	o	la
Vicia Cracca	..	o	..	..	o–lf	..	..	..	..	f–la
Lathyrus pratensis	r	o	o	..	o	..	..	..	..	..
Filipendula Ulmaria	f	..	f	..	..	lf	..	lf	..	..
Potentilla Anserina	..	o	a	..	..	o	o	f	f–la	lf
P. palustris	..	..	..	..	..	o	f	..	..	..
Parnassia palustris	..	o	..	..	..	..	..	..	o	..
Epilobium parviflorum	..	..	..	..	..	..	o	o	..	..
E. palustre	..	..	..	..	..	o	..	o	..	..
Hydrocotyle vulgaris	f	lf	o	o	..	a	..	lf	f	o
Heracleum Sphondylium	..	..	..	..	o–lf	..	..	..	..	..
Daucus Carota	..	o–lf	..	..	f	..	..	..	..	..
Galium verum	..	..	..	..	f–a	..	..	..	o	..
G. palustre	r	..	..	..	..	..	o	o	o	..
Succisa pratensis	..	o	..	f	..	..	lf	..	..	..
Bellis perennis	..	f	..	f	o–lf	..	..	..	f	o
Achillea Millefolium	..	..	..	..	f	..	..	..	..	..
Senecio Jacobaea	..	o	..	..	..	..	..	..	..	..
S. aquaticus	..	..	..	..	..	..	o	o	..	..
Leontodon autumnale	..	..	..	..	..	..	o	o	..	..
Centaurea nigra agg.	..	lf	..	..	f	..	..	..	..	..
Campanula rotundifolia	..	..	..	..	r	..	..	..	..	..
Calluna vulgaris	..	..	..	lf	..	..	..	..	..	..
Primula vulgaris	..	o	..	..	o	..	..	..	..	..
Anagallis tenella	..	..	..	lf	..	..	..	..	..	..
Menyanthes trifoliata	..	..	..	..	..	lf	..	..	f	..
Veronica scutellata	..	..	..	..	..	..	r	..	..	..
Euphrasia officinalis agg.	o	o	..	lf	..	..	..	..	o	o

TABLE I—*continued.*

Species.	var. *hebridensis.*					*latifolia.*			var. *coccinea.*	
	C. I.	C. III.	T. II.	T. I.	B. I.	C. V.	C. VI.	B. III.	C. VII.	U. III.
Pedicularis palustris	. .	. .	. .	. .	. .	f	o	f	. .	. .
P. sylvatica	. .	. .	. .	. .	. .	o	. .	o	o	. .
Rhinanthus stenophyllus	. .	. .	. .	. .	o–lf	. .	. .	o	. .	. .
Myosotis caespitosa	. .	o	. .	. .	. .	o	f	f	. .	. .
Mentha aquatica	. .	. .	. .	. .	. .	la	. .	f	o	. .
Thymus Serpyllum agg.	. .	o	. .	. .	o	. .	. .	. .	. .	. .
Prunella vulgaris	. .	la	. .	f	f	. .	. .	f	f	la
Plantago maritima	. .	. .	. .	f	o	. .	. .	. .	o	lf
P. lanceolata	. .	f	. .	f	la	o	. .	. .	f–la	f
Polygonum amphibium	. .	. .	. .	. .	. .	. .	. .	o–lf	. .	o
Rumex Acetosa	. .	. .	o	. .	o	. .	. .	. .	. .	. .
Salix repens	. .	. .	. .	. .	lf	. .	. .	. .	. .	. .
Gymnadenia conopsea	. .	o	. .	. .	. .	. .	. .	. .	. .	. .
Coeloglossum viride	. .	. .	. .	o	f	. .	. .	. .	. .	o
Platanthera bifolia	. .	o	. .	. .	. .	. .	r	. .	. .	. .
Iris Pseudacorus	. .	. .	d	. .	. .	o	. .	o–lf	o	. .
Juncus squarrosus	. .	f	. .	. .	. .	. .	. .	. .	. .	. .
J. balticus	. .	. .	. .	. .	. .	. .	. .	. .	. .	a–ld
J. conglomeratus	. .	. .	o	. .	. .	. .	. .	lf	. .	. .
J. articulatus	la	. .	. .	f	. .	a	a	a–ld	. .	lf
Luzula campestris	. .	. .	. .	. .	o	. .	. .	. .	f	o
Triglochin palustre	. .	. .	. .	. .	. .	o	o	. .	o	. .
T. maritimum	. .	. .	. .	. .	. .	f	o	. .	. .	. .
Eleocharis palustris	a	. .	. .	o	. .	la	f	lf–la	o	. .
Eriophorum angustifolium	. .	. .	. .	. .	. .	o–lf	. .	. .	. .	. .
Carex pulicaris	. .	f	. .	lf	. .	. .	. .	. .	. .	. .
C. arenaria	o	. .	. .	. .	. .	. .	. .	. .	o	lf
C. echinata	. .	a	. .	. .	. .	. .	f	o	. .	. .
C. Otrubae	o	. .	. .	. .	. .	. .	. .	. .	. .	. .
C. leporina	. .	lf	. .	. .	. .	. .	o	. .	. .	. .
C. Goodenowii	o	o	. .	o–f	. .	. .	. .	f	f	o
C. panicea	. .	lf	. .	o	. .	. .	o	f	a	o
C. flacca	. .	lf	. .	lf	. .	. .	. .	f	o	o
C. fulva	. .	. .	. .	o	o	. .	. .	. .	. .	. .
C. flava	. .	. .	. .	o	. .	o	. .	. .	a	. .
C. lasiocarpa	. .	. .	. .	. .	. .	. .	ld	. .	. .	. .
C. rostrata	o	. .	. .	. .	. .	a–ld	f	o	. .	. .
Anthoxanthum odoratum	. .	a	o	la	o	. .	lf	. .	f	ld
Alopecurus geniculatus	. .	. .	. .	. .	. .	o	o	o–lf	. .	. .
Agrostis canina	. .	. .	. .	lf	o	. .	. .	. .	. .	. .
A. alba	. .	. .	. .	. .	. .	o	. .	f	. .	. .
Holcus lanatus	o	la	lf	. .	f	o–f	o	f	f	la
Sieglingia decumbens	. .	. .	. .	f	o	. .	. .	. .	lf	. .
Phragmites communis	. .	. .	. .	. .	. .	o	o–lf	a–ld	. .	. .
Cynosurus cristatus	o	a	o	a–ld	la	o	. .	o	lf	f
Koeleria gracilis	. .	lf	. .	. .	. .	. .	. .	. .	. .	. .
Molinea caerulea	. .	. .	. .	lf	ld	o	lf	lf	. .	. .
Poa pratensis	. .	. .	. .	a	. .	o	. .	o	. .	. .
P. palustris	. .	. .	a	. .	. .	. .	. .	. .	. .	. .
P. trivialis	o	f	. .	. .	r	. .	. .	o	o	. .
Glyceria fluitans	. .	. .	o–lf	. .	. .	. .	. .	. .	. .	. .

TABLE II.

PLANT LISTS FOR HABITATS OF ORCHIS ERICETORUM (LINTON) MARSHALL ON THE ISLANDS OF COLL, TIREE, AND BARRA.

Species.	COLL. C. IV.	TIREE. T. IV.	BARRA. B. VI.
Ranunculus Flammula	o	. .	. .
Viola Riviniana	o	. .	o
Polygala serpyllacea	o	o	. .
Cerastium vulgatum	. .	o	. .
Hypericum pulchrum	. .	. .	o
Lotus corniculatus	. .	o–lf	. .
Hydrocotyle vulgaris	. .	lf	. .
Galium saxatile	o	o	o
Succisa pratensis	f	f	o
Potentilla erecta	f	f	f
Calluna vulgaris	d	a–ld	d
Erica Tetralix	f–la	a	f–la
Erica cinerea	a	f–la	lf
Anagallis tenella	. .	lf	o
Euphrasia officinalis agg.	f	f	f
Pinguicula vulgaris	o	. .	o
P. lusitanica	o	. .	. .
Pedicularis palustris	o	o	o
Prunella vulgaris	o	lf	f
Plantago maritima	. .	o–lf	o
P. lanceolata	o	o	o
Salix repens	. .	o	. .
Platanthera bifolia	o	. .	. .
Juncus squarrosus	o–lf	o	o–lf
J. articulatus	o	. .	lf
Juncus conglomeratus	o	. .	o
Luzula multiflora	. .	f	. .
Scirpus caespitosus	f	f	f
Eriophorum vaginatum	o	. .	o
E. angustifolium	f	lf	o
Carex pulicaris	f	f	o
C. echinata	la	f	f
C. flacca	f	f	f
C. panicea	la	f–la	f
C. binervis	o	o	o
C. fulva	o	o	. .
C. flava	o	f	o
Narthecium ossifragum	f	f	f
Anthoxanthum odoratum	o	la	o
Agrostis tenuis	o–lf	lf	f
Holcus lanatus	o	lf	f
Sieglingia decumbens	f	f	o–lf
Cynosurus cristatus	o	a	o
Molinia caerulea	ld	a–ld	a
Festuca ovina	o	a	o–lf
Nardus stricta	a–ld	a–ld	ld
Blechnum spicant	o	. .	o

Fuchsii var. *hebridensis* is overwhelmingly the commonest orchid, a few plants of *O. latifolia* occur in the wetter zones, and outliers of the *O. ericetorum* colonies, characteristic of the moorland, appear on the rock outcrops. No hybrids were detected.

Stature: Mean, 19·21 cm.; Standard Deviation, 4·29 cm.; Range, 13–36 cm.

Population C. III. Machair edge, Cornaig Beg. This habitat is of the same nature as the previous one, differing only in being enclosed and not subject to grazing. The meadow is cut for hay in late August, but otherwise is untouched by man. Soil-pH at tuber depth ranges narrowly about 5·5. *O. Fuchsii* var. *hebridensis* is again the most abundant orchid, and comprises 98 per cent. of the total individuals. Occasional plants of *Platanthera bifolia* are present, and rock outcrops here support *Gymnadenia conopsea*. There is no sign of hybridity.

Stature: Mean, 21·01 cm.; Standard Deviation, 4·99 cm.; Range, 14–38 cm.

TIREE.

Population T. I. Lightly grazed open grassland west of Scarinish. The habitat is again semi-natural, bordering the stabilised machair which is extensively cultivated on Tiree. The soil is a moderately moist, sandy humus, pH as follows: 1st plant, 5·5; 25th plant, 5·8; 50th plant, 5·5; 75th plant, 5·7; 100th plant, 6·0. *Cynosurus cristatus* and *Anthoxanthum odoratum* are co-dominant over the area. The present species is most plentiful; although locally, particularly inland, *O. ericetorum* forms extensive colonies. Hybrid individuals are not unusual.

Stature: Mean, 20·40 cm.; Standard Deviation, 4·89 cm.; Range, 11–42 cm.

Population T. II. Large *Iris Pseudacorus* bed east of Gott Manse. *O. Fuchsii* var. *hebridensis* frequently grows in association with irises, and is particularly prominent in this extensive bed. Soil-pH at tuber depth is fairly uniformly 5·8. There are no other orchids present.

Stature: Mean, 33·49 cm.; Standard Deviation, 6·25 cm.; Range, 20–52 cm.

Population T. III. Machair edge, Balephetrish. This habitat corresponds in detail with that of the Coll population C. III, being a section of stabilised machair enclosed for hay. The soil is a moist sandy humus, with a pH at tuber depth uniformly 5·5. A small admixture of *O. latifolia* (less than 1 per cent.) is evident in wetter areas. No hybrids were detected.

Stature: Mean, 19·31 cm.; Standard Deviation, 4·38 cm.; Range, 13–37 cm.

BARRA.

Population B. I. Ungrazed open grassland, Kinloch (head of Loch St. Clair). This is again a machair edge habitat. Soil-pH ranges between 5·8 and 6·0. There is little interference on the part of man except in the cutting of hay. *O. Fuchsii* var. *hebridensis* is extraordinarily abundant in such localities as this everywhere in the west of Barra. *O. latifolia* is occasional in the damper regions; apart from *Coeloglossum viride*, no other orchids occur.

Stature: Mean, 22·61 cm.; Standard Deviation, 4·28 cm.; Range, 14–38 cm.

Population B. II. Ungrazed, moist dune flat, south end of Eoligarry Bay. Again a "natural" habitat, enclosed and cut occasionally for hay. Soil-pH as follows: 1st plant, 5·8; 25th plant, 5·5; 50th plant, 5·5; 75th plant, 5·3; 100th plant, 6·0. No other orchids occur.

Stature: Mean, 25·26 cm.; Standard Deviation, 4·93 cm.; Range, 15–39 cm.

SOUTH UIST.

Population U. I. Damp, lightly grazed meadow, Askernish machair. The habitat is equivalent ecologically to that of the Barra population B. I. The soil is again a moderately damp, sandy humus, pH 5·5–6·0. *O. latifolia* is thinly distributed throughout the area, comprising about 3 per cent. of the total individuals present.

Stature: Mean, 28·43 cm.; Standard Deviation, 5·07 cm.; Range, 19–43 cm.

O. ericetorum (Linton) Marshall.

COLL.

Population C. IV. Heather moorland near Arnabost Farm. Much of the moorland of Coll has been recently fired, and this area has been selected for sampling as providing an example of the association which has not yet suffered serious interference.

The area is clad with thin peat, with an average pH of 4·7. Saturated *Sphagnum*-filled hollows occur, but the greater part of the zone is only moderately moist. *O. ericetorum* is the only orchid, sparsely distributed, as it is over great areas of such moorland throughout the Hebrides. There is slight grazing by sheep.

Stature: Mean, 20·90 cm.; Standard Deviation, 4·19 cm.; Range, 13–36 cm.

TIREE.

Population T. IV. Moderately moist heather moor, neighbourhood of Loch Caol. Tiree has been thoroughly de-peated, and the present locality typifies the mixed heather moorland which has succeeded the peat bogs. The soil-pH varies between 4·7 and 4·9. No other orchids are present.

Stature: Mean, 16·21 cm.; Standard Deviation, 3·21 cm.; Range, 10–24 cm.

BARRA.

Population B. VI. Heather moorland, slopes of Ben Tangaval. *Calluna*-heath on moderately moist, thin peat cloaks the greater part of the Archaean gneisses of Barra, and again *O. ericetorum* is a universal if somewhat thinly distributed component of the association. Soil-pH varies between 4·6 and 4·9. No other orchids are present.

Stature: Mean, 18·99 cm.; Standard Deviation, 3·55 cm.; Range, 11–26 cm.

O. latifolia L. (sec. Pugsley).

COLL.

Population C. V. Floor of wet dune hollow, west of Cliad. *Carex rostrata* is the dominant vascular species of the greater part of this area, which is partially submerged, at least in the early months of the year. The pH of the surface water is 6·6. *O. latifolia* is the only orchid occurring in the *Carex rostrata* zone, although *O. Fuchsii* var. *hebridensis* is plentiful in the drier marginal regions.

Stature: Mean, 24·54 cm.; Standard Deviation, 6·19 cm.; Range, 15–39 cm.

Population C. VI. Marshland near the lodge, Arinagour. This marsh occupies the valley floor between the end of Loch an Duin and the Arinagour-Kilbride road, and is the type of inland locality frequently favoured by *O. latifolia*. The surface of the marsh is somewhat uneven, and the species is most abundant in the neighbourhood of stretches of open water. pH ranges between 5·8 and 6·0.

Stature: Mean, 21·29 cm.; Standard Deviation, 3·83 cm.; Range, 14–35 cm.

BARRA.

Population B. III. Marshland, northern and western shores of Loch St. Clair. The species occurs in a belt between the reed swamp, which intermittently fringes the loch, and the drier machair. This is the type of habitat favoured by the species throughout the Outer Hebrides. At the west end of the loch pH readings were regularly 6·7; in the east, 6·3. *Orchis Fuchsii* var. *hebridensis* is abundant in the drier areas around the loch except on the southern shore, and isolated specimens occur in the area of *O. latifolia*. *O. purpurella* is thinly distributed at the eastern end. Two plants of undoubtedly hybrid origin (*O. latifolia* × *Fuchsii* var. *hebridensis*) were located in this region.

Stature: Mean, 23·44 cm.; Standard Deviation, 5·10 cm.; Range, 13–40 cm.

Population B. IV. Marsh, S.W. extremity of Loch an Duin. The occurrence of this isolated colony of *O. latifolia* away from the machair is correlated with a relatively high soil-pH: 5·8. No other orchids are present in the marsh itself, although marginally in the south *O. ericetorum* abounds, and along the road which skirts the north of the loch *O. Fuchsii* var. *hebridensis* is occasional.

Stature: Mean, 19·45 cm.; Standard Deviation, 3·85 cm.; Range, 15–29 cm.

SOUTH UIST.

Population U. II. Marsh, north end of Loch Hallan. The conditions here practically duplicate those of the Barra population B. III from Loch St. Clair, the orchids being abundant in the broad belt between the *Scirpus Tabernaemontani*–*Phragmites communis* reed-swamp and the area of machair cultivation where *O. Fuchsii* var. *hebridensis* predominates. pH of soil water is 6·4.

Stature: Mean, 23·02 cm.; Standard Deviation, 4·83 cm.; Range, 16–33 cm.

O. latifolia L. var. **coccinea** Pugsl.

COLL.

Population C. VII. Level machair, in the lee of the mobile dunes, A Croic. The orchid colony is several acres in extent, and covers an area dotted with shallow lochs choked with *Chara* spp. Determinations of the pH of the moist sandy zones preferred by the variety gave results ranging from 6·8 to 7·2. The whole area is subject to light grazing by sheep and cattle. *O. Fuchsii* var. *hebridensis* occurs occasionally in drier regions, and hybrids (probably *O. Fuchsii* var. *hebridensis* × *latifolia* var. *coccinea*) were located on the outskirts of the *latifolia* colony.

Stature: Mean, 12·29 cm.; Standard Deviation, 2·73 cm.; Range, 6–20 cm.

BARRA.

Population B. V. Damp-floored blow-out in stabilised machair, Borve. This is the characteristic habitat for the variety in the Outer Hebrides: on calcareous dune sand subject to occasional flooding but with slight humous content only, and retaining little moisture. Soil-pH is relatively high, varying between 7·0 and 7·6. Occasional plants of *O. Fuchsii* var. *hebridensis* occur.

Stature: Mean, 12·22 cm.; Standard Deviation, 2·97 cm.; Range, 6–17 cm.

SOUTH UIST.

Population U. III. Floor of large machair blow-out, Daliburgh. This is an example on a considerably larger scale of the type of habitat described above for the Barra population B. V. The floor of the blow-out, several acres in extent, is quite level, moderately moist, and dotted with ephemeral pools. Over a considerable area *Juncus balticus* is the dominant or co-dominant vascular species. Soil-pH varies between 6·8 in the *Juncus balticus* zones to 7·6 around the pools. No other orchids are present.

Stature: Mean, 10·80 cm.; Standard Deviation, 2·42 cm.; Range, 6–16 cm.

The Analysis of Characters.

Leaf Number.

In determining the number of leaves per plant, the lowest green leaf above the tuber has been counted as the first, and that below the first bract as the last, even although it may be scale- or bract-like in appearance.

Table III.

Distribution of Number of Leaves per Plant in O. Fuchsii var. hebridensis, O. ericetorum, O. latifolia, and O. latifolia var. coccinea on the Islands of Coll, Tiree, Barra, and South Uist. Percentage in each class to first decimal place.

Population.	Number of Leaves.									
	3	4	5	6	7	8	9	10	11	12
var. *hebridensis*:										
Coll I . . .	..	..	11·1	25·9	42·7	14·8	4·6	..	0·9	..
II . . .	..	2·1	9·4	35·4	38·6	8·3	4·2	2·1	..	..
Tiree I . .	..	1·4	6·5	35·6	42·1	8·8	3·2	0·9	1·4	..
II . .	..	..	12·6	38·0	35·6	8·0	4·6	1·2	..	..
Barra I . .	..	1·9	9·6	36·6	34·6	14·4	2·9	..	..	..
II . .	..	1·0	8·6	30·5	40·0	13·2	3·8	1·9	1·0	..
South Uist I . .	..	2·8	15·5	40·8	26·8	11·3	2·8	..	..	..
ericetorum:										
Coll IV . . .	0·5	4·1	36·6	39·6	15·7	3·0	0·5	..	..	..
Tiree IV . .	..	6·5	36·6	31·9	19·9	4·2	0·9	..	..	..
Barra VI . .	..	4·8	30·7	41·9	17·8	4·8	..	..	..	..
latifolia:										
Coll V . . .	..	3·5	33·3	49·5	12·7	1·2	..	..	..	..
Barra III . .	..	0·9	28·9	39·5	19·3	7·8	1·7	1·7	..	..
S. Uist II . . .	..	2·3	35·4	46·9	13·8	..	0·8	0·8	..	..
latifolia var. *coccinea*:										
Coll VIII . .	2·8	35·2	46·3	14·8	0·9	..	..	..	..	..
Barra V . .	2·7	34·0	37·3	23·3	2·7	..	..	..	..	..
S. Uist III . .	5·3	38·6	47·4	8·8	..	..	..	..	..	..

Table III reveals a distinction between *O. Fuchsii* and *O. ericetorum* in leaf number. Whereas of the former some 70 per cent. of individuals possess 6 or 7 leaves, approximately the same percentage of the latter possess 5 or 6 leaves. Within the subspecies none of the variations from population to population has any statistical significance.

Surprisingly enough, despite the considerable difference in mean plant stature between the two varieties of *O. latifolia*, their modal classes for leaf number are but one apart: *latifolia*, 6; *latifolia* var. *coccinea*, 5.

Leaf Marking.

Variation both in intensity and form of leaf marks is normal in populations of the *maculata* complex. Patterns of pin-point dotting, random spotting, regular bars and blotches, and in a few rare cases of green-centred ring spots feature in both *O. ericetorum* and *Fuchsii*. To assess total pigmentation, five arbitrary intensity grades have been taken: Nil, Light, Medium, Heavy, and Very Heavy. Individual plants have been referred to the appropriate grade by the visual impression gained by examination of the largest unwithered leaf. No account has been taken of spot shape; thus, for example, in the "Light" category plants possessing minute markings have been placed, as well as those with large but faint markings. The value of this character for statistical purposes is limited by the small number of classes. Since the assessment is a matter of personal judgment, multiplication of their number would lead merely to an increased possibility of error in the absence of a more precise scale of comparison.

Leaf marking is rare in *O. latifolia*, although one or two of the Coll populations of this species possess individuals with the fine pin-point dotting reminiscent of *purpurella*. Since these populations contain, or adjoin, *purpurella* colonies, the possibility of a hybrid origin of this character exists.

The outstanding fact which emerges from Table IV is that while *O. Fuchsii* var. *hebridensis* on Coll and Tiree possesses something like one plant in ten with totally unmarked leaves, only a very small percentage indeed of Outer Island plants are unmarked. If, as is the case in many spotted-leaved plants (*Arum maculata*, *Plantago maritima*), the absence of leaf markings is a recessive condition in *O. Fuchsii*, this indicates an almost complete absence of the recessive gene from the Outer Islands. Noticeable, also, is the general shift of the distribution curve towards more intense marking, exemplified by the doubling of the percentage of individuals in the "Heavy" class in the Outer Isles.

If the distribution curves for *O. ericetorum* are treated statistically as "normal," then the samples from Coll, Tiree, and Barra (about 200 each) reveal no significant difference in population structure.

TABLE IV.

FREQUENCY DISTRIBUTION OF LEAF SPOT CLASSES FOR O. FUCHSII VAR. HEBRIDENSIS AND O. ERICETORUM, ON THE ISLANDS OF COLL, TIREE, BARRA, AND SOUTH UIST.

Population.	Leaf Spot Classes.				
	1	2	3	4	5
var. *hebridensis*:					
Coll I.	12·7	36·4	34·6	11·8	4·5
II.	12·5	35·4	34·4	13·6	4·2
III.	12·6	38·7	31·5	12·6	4·7
Tiree I	10·2	39·8	35·2	11·6	3·2
II	6·0	31·0	36·9	20·1	6·0
III	9·1	26·2	36·4	25·0	3·4
Barra I	..	25·5	27·4	35·3	11·8
II	0·9	29·6	33·3	28·6	7·6
S. Uist I	..	26·0	43·8	21·9	8·2
ericetorum					
Coll IV.	25·2	41·8	25·2	5·8	1·9
Tiree IV	37·2	36·2	20·0	5·7	1·0
Barra VI	16·7	38·2	33·8	9·8	1·5

This treatment is not, of course, justified if *absence* of leaf markings is a simple recessive. In such an event, the fact that the "No Spot" class contains twice as great a percentage of individuals on the Inner Islands as the same class on Barra may indicate variation in this character in *O. ericetorum* paralleling variation in the same character in *O. Fuchsii.*

Flower Colour.

The Dactylorchids fall into two main flower colour groupings: a deep purple-lilac-white series, to some stage in which *O. purpurella* and the various forms of the *maculata* complex can be referred, and a maroon or crimson-red *via* salmon- or flesh-pink to white series in which the *latifolia* varieties fall. Where an index of colour *intensity* of an individual is required, a highly exact match for *shade* is not an essential. It has thus been possible to match all the colours met in field populations on two logarithmically stepped colorimeters.

In the preparation of these, an initial match to the deepest shade encountered was obtained by arbitrary mixture of laboratory stains (safranin and "Quink" writing fluid in suitable proportions provide an excellent match). From this a dilution series with a dilution-factor of 1·5 (fig. 1) was prepared. The actual colorimeter used in the field consisted of a series of filter-paper strips immersed in each of the stain-dilution series, dried, bound on to a conveniently sized tube, and faced with transparent adhesive tape. In use it was found possible to refer any flower rapidly to the appropriate step by placing the labellum in contact with the scale and comparing at arm's length in good light.

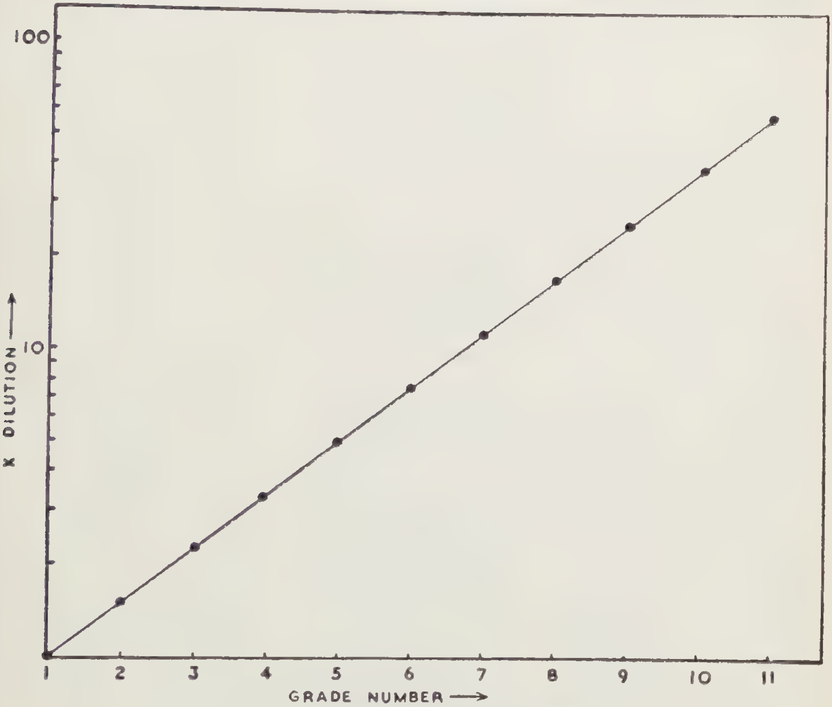

FIG. 1.—Scaling of flower colorimeter.

The flowers of the orchid inflorescence open in acropetal succession, and there is generally a slight intensification of colour up to anthesis. To establish uniformity from plant to plant the lowest mature flower still possessing pollinia was selected for comparison. In all cases matching was made to the ground colour of the labellum, the intensity of pattern being ignored. Since, particularly in *O. Fuchsii* var. *hebridensis*, the labellum centre is often somewhat lighter in tone than the lateral wings, comparison was restricted to the marginal shade.

Table V.

Frequency Distribution of Flower Colour Grade for Orchis Fuchsii var. hebridensis and O. ericetorum on the Islands of Coll. Tiree. Barra, and South Uist. Percentage in each grade to second decimal place.

Population.	Colour Grade.												
	1	2	3	4	5	6	7	8	9	10	11	12	13
var. *hebridensis*:													
Coll I . . .	. .	2·50	5·00	6·66	30·00	28·34	15·83	5·84	4·16	1·67	. .	. .	. .
II . . .	. .	1·00	4·00	7·00	32·00	30·00	15·00	6·00	3·00	1·00	1·00	. .	. .
III . . .	. .	2·36	8·67	13·38	29·91	22·84	12·60	6·30	3·15	0·79	. .	. .	. .
Tiree I . . .	. .	1·19	5·36	16·08	25·00	23·80	13·69	8·94	2·38	2·38	1·19	. .	. .
II . . .	. .	1·14	4·54	6·82	22·72	35·24	22·72	4·54	1·14	1·14	. .	. .	. .
III . . .	. .	1·19	4·76	10·72	28·55	26·20	21·44	5·95	1·19	. .	. .	. .	. .
Barra I . . .	. .	4·81	9·62	16·35	25·95	22·12	13·45	3·85	2·88	0·96	. .	. .	. .
II . . .	. .	1·82	7·27	13·63	27·27	29·09	9·09	8·18	3·63	0·91	. .	. .	. .
S. Uist I . . .	. .	0·96	6·73	12·50	27·89	25·95	10·58	6·73	5·77	1·92	0·96	. .	. .
Numerical Totals: All Samples (1106 plants) . .	. .	20	67	126	310	298	161	71	34	14	5	. .	. .
ericetorum:													
Coll IV . . .	. .	. .	. .	. .	3·89	7·79	5·19	9·09	20·77	22·08	15·58	5·84	9·75
Tiree IV . . .	. .	. .	. .	. .	3·93	5·88	7·84	8·83	14·71	26·47	12·74	8·82	10·78
Barra VI . . .	. .	. .	. .	0·52	6·26	7·81	7·29	10·93	17·17	28·15	12·50	7·81	1·56
Numerical Totals: All Samples (550 plants) . .	. .	. .	. .	1	26	39	38	53	96	142	73	42	40

TABLE VI.

FREQUENCY DISTRIBUTION OF FLOWER COLOUR GRADE FOR ORCHIS LATIFOLIA AND O. LATIFOLIA VAR. COCCINEA ON THE ISLANDS OF COLL, BARRA, AND SOUTH UIST. PERCENTAGE IN EACH GRADE TO SECOND DECIMAL PLACE.

Population.	Colour Grade.												
	1	2	3	4	5	6	7	8	9	10	11	12	13
latifolia :													
Coll V, VI . . .	. .	. .	. .	. .	. .	5·00	6·67	10·00	45·00	20·00	11·67	1·67	. .
Barra III, IV . .	. .	. .	1·02	. .	4·08	19·39	9·18	17·36	28·58	14·29	4·08	2·02	. .
S. Uist II . . .	. .	. .	. .	1·87	4·67	12·16	14·02	20·55	18·70	19·63	7·48	0·93	. .
latifolia var. *coccinea :*													
Coll VIII . . .	. .	2·93	22·32	33·96	12·62	15·54	4·85	7·77	. .	. .	. .	. .	. .
Barra V . . .	. .	1·00	17·00	25·00	33·00	17·00	4·00	2·00	1·00	. .	. .	. .	. .
S. Uist III. . .	. .	. .	14·83	30·90	33·27	16·06	3·70	. .	1·23	. .	. .	. .	. .

The extraordinary diversity of flower colour found in the *maculata* complex is plain, as is also the colour distinction between var. *hebridensis* and *ericetorum*. In the former some 50 per cent. of individuals lie in grades 5 and 6; in the latter about the same percentage in grades 9, 10, and 11 on the same scale.

Table VI makes clear the overlapping but distinct colour ranges of *O. latifolia* and its variety *coccinea*; the former salmon- or flesh-coloured, the latter maroon.

Tables V and VI show no regional differentiation for labellum colour of statistical significance for any of the species and varieties.

Labellum Shape.

The expression of the shape of an organ in numerical terms is often one of the main difficulties in devising biometrical technique, for, as Anderson has pointed out in connection with his analysis of Iris populations (1936), the precisely descriptive terminology of taxonomy can often express differences between the forms of parts which fail completely to stand out in elaborate tables of measurements of the same parts. In the present case there is no simple grouping of measurements which is capable of expressing *all* the variation in form of labellum met with in the *maculata* complex; the problem becomes one of selecting those measurements which express that part of the variation which is of greatest taxonomic significance.

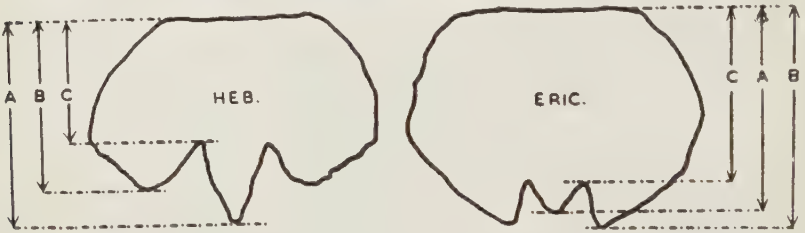

FIG. 2.—Typical labellum shapes in *O. Fuchsii* and *O. ericetorum*, showing dimensions employed in deriving shape index.

Typical labellum shapes encountered in the two species, *O. Fuchsii* and *O. ericetorum*, are shown in fig. 2. The shape index adopted is the ratio $\frac{2A}{B+C}$, the measurements having the significance indicated in the figure. The base from which these measurements are taken is conveniently the point at which the spur merges into the labellum. In brief, the use of this index amounts to the comparison of the extreme length of the median lobe of the tri-lobed lip with the mean of the length of the lateral lobes and the distance between the point of deepest incision and the spur-mouth.

The dimensions A, B, and C are readily determined from lips mounted in the manner previously described if the original cut has been made precisely at the spur-mouth, or if the position of the spur-mouth is discernible on the dried organ. Bilateral asymmetry is met with occasionally. In such cases measurements have been taken exclusively from the right-hand side of the labellum observed from the front of the flower.

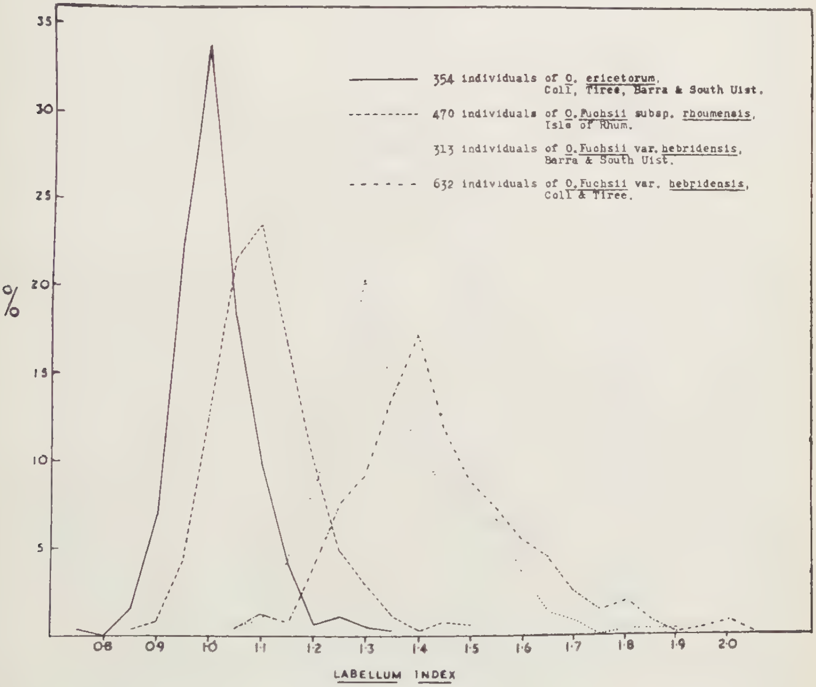

FIG. 3.—Variation polygons for labellum shape index in the *maculata* complex.

Clearly, in the case of individuals referable to *O. Fuchsii*, the index will have a value greater than unity (usually approximating to 1·4), and in the case of *O. ericetorum*, where the central lobe is frequently shorter than the laterals, a value in the neighbourhood of unity. In practice, the use of this index with *O. Fuchsii* material tends to produce a skew variation curve tailing towards extreme values, suggesting that the growth system is too complex to be resolved in a simple linear manner. Nevertheless, the primary desideratum is realised, in that the distinction between the various labellum forms met in the *maculata* complex is clearly brought out in the variation polygons.

Table VII incorporates the computations of labellum shape index for the Coll, Tiree, Barra, and South Uist populations of *ericetorum* and var. *hebridensis*, and Table IX those for the Rhum form of *O. Fuchsii*. In figs. 3, 4, and 5, variation polygons for the various populations of these types are superimposed.

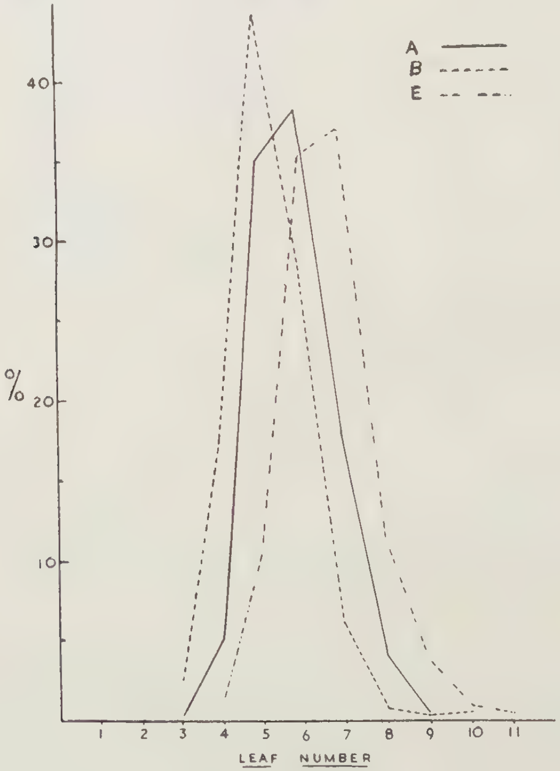

Fig. 4.—Variation polygons for leaf number.
A. *Orchis ericetorum*, Coll, Tiree, Barra.
B. *O. Fuchsii* subsp. *rhoumensis*, Isle of Rhum.
E. *O. Fuchsii* var. *hebridensis*, Coll, Tiree, Barra, South Uist.

A slight divergence is apparent between the Coll and Tiree populations of *O. Fuchsii* var. *hebridensis* and those of the Outer Isles; the modal class for the former is 1·375–1·425, for the latter 1·275–1·325. With the scatter as great as it is, this difference just fails to achieve statistical significance. Nevertheless, a difference in labellum form between populations from the two groups of islands is apparent to the eye (see Pls. I and II); in a large and representative group of lips the more slenderly dissected Coll and Tiree populations can be detected.

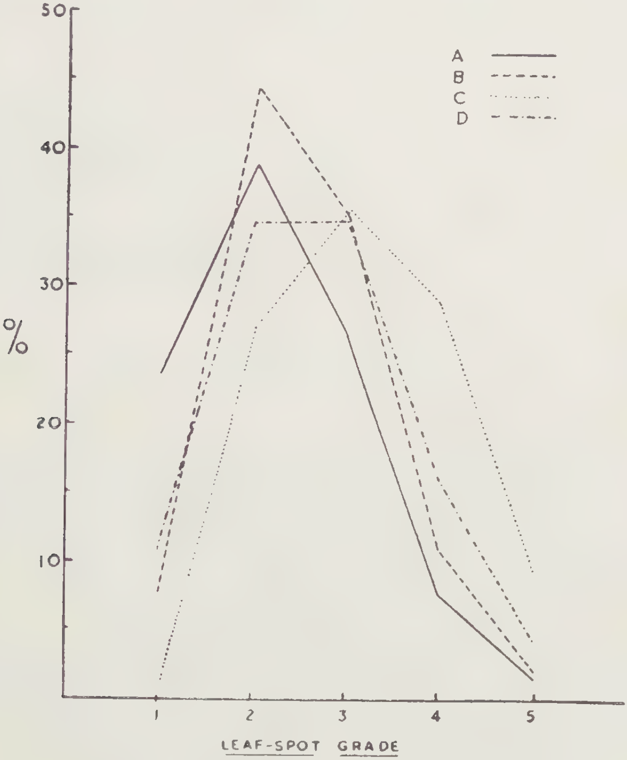

Fig. 5.—Variation polygons for leaf-spot grade.

A. *Orchis ericetorum*, Coll, Tiree, Barra.
B. *O. Fuchsii* subsp. *rhoumensis*, Isle of Rhum.
C. *O. Fuchsii* var. *hebridensis*, Barra and South Uist.
D. *O. Fuchsii* var. *hebridensis*, Coll and Tiree.

Flower Number.

The determination of the number of flowers in the inflorescence is a straightforward, if tedious, process. The most rapid technique in dealing with a large sample is to remove each flower in turn complete with bract by a downward tearing motion, starting with the lowest flowers. All the flower primordia are usually found to

TAB

LABELLUM-SHAPE INDEX DISTRIBUTIONS FOR ORCHIS FUCH
TIREE, BARRA, AND SOUTH UIST. PERCE

Population.	Class Cent												
	0·75	0·80	0·85	0·90	0·95	1·00	1·05	1·10	1·15	1·20	1·25	1·30	1·
var. *hebridensis* :													
Coll I .	..	..	..	..	..	..	..	1·81	..	5·45	10·91	10·91	13·
II .	..	..	..	..	..	..	1·00	2·00	3·00	4·00	8·00	9·00	11·
III .	..	..	..	..	..	..	..	1·00	1·00	7·00	10·00	9·00	17·
Tiree I .	..	..	..	..	..	..	1·72	1·72	0·86	3·45	3·45	6·04	13·
II .	..	..	..	..	..	..	..	..	..	2·91	7·77	7·77	12·
III .	..	..	..	..	..	..	..	..	..	1·33	4·00	9·34	12·
Barra I .	..	..	..	..	..	..	0·86	0·86	6·03	12·92	13·79	25·87	13·
II .	..	..	..	..	..	..	..	1·00	3·00	4·00	11·00	17·00	15·
S. Uist I .	..	..	..	..	..	..	1·00	1·00	3·00	7·00	12·00	17·00	14·
ericetorum :													
Coll IV .	..	..	1·16	8·14	19·20	26·75	20·36	12·78	6·98	2·33	1·74	..	0·
Tiree IV .	1·03	..	2·06	8·24	22·68	33·00	20·62	9·28	1·03	..	1·55	..	0·
Barra VI .	..	..	1·49	4·48	25·38	41·79	13·43	7·47	4·48	..	..	1·49	.

have been developed by the time that the basal ones have begun to open, even although stem elongation may still be in progress. Thus no inaccuracy is introduced by using young inflorescences provided that all buds are counted.

TABLE VIII.

NUMBER OF FLOWERS IN THE INFLORESCENCE: O. LATIFOLIA, COLL, BARRA, SOUTH UIST; O. LATIFOLIA VAR. COCCINEA, COLL, BARRA, SOUTH UIST; O. FUCHSII VAR. HEBRIDENSIS, COLL, BARRA, TIREE, SOUTH UIST; O. FUCHSII SUBSP. RHOUMENSIS, ISLE OF RHUM; O. ERICETORUM, COLL, TIREE, BARRA.

	Mean.	Standard Deviation.	Range.
O. latifolia	17·68	6·12	8–42
O. latifolia var. *coccinea* . .	16·92	6·31	9–40
O. Fuchsii var. *hebridensis* . .	23·79	6·17	12–52
O. Fuchsii subsp. *rhoumensis* .	12·71	3·89	7–39
O. ericetorum	15·11	4·06	8–29

Flower number is a highly variable factor in the Dactylorchids, and one which is apparently independent of the operation of habitat factors. The population parameters of Table VIII are derived

VII.

VAR. HEBRIDENSIS AND O. ERICETORUM ON THE ISLANDS OF
AGES IN EACH CLASS TO SECOND DECIMAL PLACE.

(Class Interval, 0·05).

1·40	1·45	1·50	1·55	1·60	1·65	1·70	1·75	1·80	1·85	1·90	1·95	2·00	2·05	2·10	2·15
16·36	13·73	4·55	3·63	4·55	1·81	1·81	3·63	..	..	..	..	..	1·81	1·81	..
15·00	10·00	10·00	9·00	5·00	4·00	4·00	1·00	2·00	1·00	..	..	1·00	..	..	..
18·00	11·00	7·00	5·00	4·00	4·00	1·00	1·00	2·00	1·00	..	..	1·00	..	..	..
19·82	11·21	10·34	7·76	6·04	3·45	1·72	2·58	1·72	1·72	..	0·86	1·72	..	..	..
17·47	11·65	11·65	9·72	5·83	5·83	2·91	0·97	0·97	0·97	0·97	..	..	..	..	..
16·00	14·68	10·66	9·34	6·67	5·34	2·67	2·67	..	..	1·33	1·33	1·33	1·33	..	..
7·76	7·76	3·45	3·45	2·59	0·86	..	..	..	..	..	..	..	..	..	..
14·00	9·00	9·00	8·00	4·00	1·00	2·00	..	..	1·00	1·00	..	..	..	..	..
11·00	9·00	8·00	9·00	4·00	2·00	1·00	..	1·00	..	..	..	..	..	..	..

from a consolidation of the data from certain of the populations of *latifolia*, *latifolia* var. *coccinea*, *ericetorum*, and *Fuchsii* var. *hebridensis* on the islands indicated.

The difference in mean flower number between *latifolia* var. *coccinea* and the type is not significant. There is, however, a clear differentiation between *O. Fuchsii* var. *hebridensis* and *ericetorum* for this factor.

Orchis Fuchsii Druce on the Isle of Rhum.

The presence of an anomalous form of the *maculata* complex on Rhum was first observed and commented upon by J. W. Heslop Harrison in 1937. Originally regarded as a form of *O. ericetorum*, this plant has a flowering period which reaches a peak in mid-August, that is, a month to six weeks later than the peak flowering period for *O. ericetorum* elsewhere in the Hebrides. Thus, when the writer left the Outer Hebrides in 1947 in the first week in August, *ericetorum* there was practically over, as for that matter was *O. latifolia*; *Fuchsii* was in rapid decline and *O. latifolia* var. *coccinea* (which has a somewhat more protracted flowering period than the type) was well advanced. In contrast, the Rhum plant was in early flower, and reached a peak during the following week.

The biometrical analysis of this form, which is apparently endemic to Rhum, was made from a collection of more than a thousand individuals drawn from populations in Harris Glen, Glen Shelesder, Upper Kilmory Glen, and about the Long Loch. It is in these localities that the form is most abundant; not, however, in isolated colonies, since the plant is thinly distributed over the centre of the island, providing thereby a genetic link between the profuse glen populations. Statistical tests reveal no significant divergence between collections from the various localities, and the biometric data from all sources have therefore been consolidated.

The characters of leaf number, leaf marking, stature, flower number, and labellum shape are analysed in Table IX in the manner previously employed. The modal class for flower colour is 7.

For a clear appreciation of the position of this Rhum form in relation to the other forms of the *maculata* complex in the Hebrides,

TABLE IX.

CHARACTER ANALYSIS OF O. FUCHSII SUBSP. RHOUMENSIS. COLLECTIONS FROM HARRIS GLEN, GLEN SHELESDER, LONG LOCH, AND KILMORY GLEN, ISLE OF RHUM. PERCENTAGE IN EACH CLASS.

	Grades.				
	1	2	3	4	5
Leaf Marking	7·75	44·44	35·05	10·86	1·90

	Number.								
	3	4	5	6	7	8	9	10	11
Leaf Number	2·38	17·27	43·90	28·59	6·19	0·83	0·36	0·48	. .

	Class Centres.												
	0·85	0·90	0·95	1·00	1·05	1·10	1·15	1·20	1·25	1·30	1·35	1·40	1·45
Labellum Shape Index	0·37	0·75	4·11	12·69	21·64	23·50	16·79	10·07	4·85	2·98	1·12	0·37	0·75

Plant Stature: Mean, 17·97 cm.; Mean Deviation, 5·08; Range, 10–38 cm.

Fuchsii and *ericetorum*, a comparison of variation ranges for the characters for which numerical data are available in the three types is necessary. Superimposed variation polygons are presented in figs. 3, 4, and 5. The *Fuchsii* and *ericetorum* curves are derived from a consolidation of the majority of the observations made on these forms for the characters concerned on Coll, Tiree, Barra, and South Uist: those for the Rhum form are drawn from Table IX.

In its distribution on Rhum this orchid shows a tolerance range coincident neither with that of *O. Fuchsii* nor *O. ericetorum*. It consistently shuns the peaty areas, and the localities which it inhabits in profusion are all of the nature of extended ecotones, in which soil-pH is influenced to a greater or less degree by blown sand. Nevertheless, the plant is not truly a machair form, and it is absent from the machair areas of lower Kilmory Glen, Harris, and Samhnan Insir.

This characteristic of intermediacy between *O. Fuchsii* and *O. ericetorum*, expressed in a range of morphological and physiological attributes, made it a matter of importance that its chromosome number should be established.

For this purpose, young leaves, root and tuber tips were fixed in the field in Lewitski's solution. Sections were cut at 12 μ, and stained by the iodine-gentian-violet method of Newton. No satisfactory plates were obtained from young leaves. The chromosomes in root-tip preparations were found to be small and somewhat difficult to count, although fixation appeared satisfactory. The somatic chromosome number was determined as 40.

It is thus clear that there exists on the Isle of Rhum an orchid of the *maculata* complex, falling into line cytologically with *O. Fuchsii*, in the diploid series, which possesses an assemblage of characters suggesting morphological and physiological intermediacy between *O. Fuchsii* and *ericetorum*. Whether the plant is the stabilised product of ancient hybridity between isolated strains of the two more widely spread forms of the *maculata* complex, or whether it is of earlier origin than either, must for the moment, at least, remain undecided. Its occurrence on Rhum, an island noted for the relict forms in its flora, would certainly seem significant.

In the interim the plant is here described as a subspecies of *O. Fuchsii* Druce, in recognition of its cytological affinities.

Orchis Fuchsii Druce.

subsp. *rhoumensis* Heslop-Harrison f., subsp. nov. Altitudo 10–38 cm.; tubera similia atque *O. Fuchsii* Dr.; folia quam in *O.*

Fuchsii angustiora, maculis parvis subnigris notata; spica 10–15-flora; flores pallide purpurei; labellum trilobatum, lobo medio parvo, triangulo, saepe breviori lateralibus rotundatis latis; calcar gracile.

Chromosomata: $2n = 40$.

Floratio ineunte Augusto.

Hab. Isle of Rhum.

O. Fuchsii Druce subsp. *rhoumensis* is so far known only from the island of Rhum, where it expresses a tolerance range of soil-pH extending from 4·9 to 5·5. The tubers are stout, 4-palmatifid and divergent; mean stem length is 18 cm., the bulk of plants lying between 10 and 30 cm. The stem is solid, and somewhat more slender than in *O. Fuchsii.* The mean leaf number is 5; the basal leaves being narrow, keeled and folded, and characteristically lightly spotted. The flower colour is variable, but on the average somewhat less intense than in *O. Fuchsii* var. *hebridensis.* Typically the labellum is about as broad as long, with a median lobe small and often shorter than the broadly spreading laterals, a feature which distinguishes the plant immediately from *Fuchsii* forms. The labellum patterning is normally strongly marked, formed of paired loops of pigment continuous or dissociated into bars and dots. The lateral sepals are normally poised forward, matching the labellum in colour, and obscurely marked in about 40 per cent. of cases with dark dots or rings. The spur is invariably slender and pointed, a feature in which the plant differs markedly from *O. Fuchsii.*

Holotype, in Herb. Edin.

Dactylorchid Labellum Pattern.

The forms of the *maculata* complex display a considerable diversity of lip patterning, based upon a theme of dots, bars, and lines of purple or reddish pigment superimposed upon a lighter lilac or white ground colour. Superficially the system would appear beyond analysis; in actuality, when the various types are broken down, a regular basis of organisation is generally apparent. The functional system seems to be of the same order as that demonstrated by Kuehn and Henke (1936) for wing patterning in the Flour Moth, *Ephestia kuehniella*: a "determination stream," emerging upon the organ during development in a precisely orientated manner, following a path in part related to the existing venation, and leaving that path visible in the mature organ in the form of pigment "flow-lines."

This concept applied to the orchis labellum is illustrated in diagrams A–F in fig. 7.

The two points of initiation appear to be located at the mouth of the spur: individuals with the pattern restricted to two spots of pigment in this region are not uncommon. From thence two loops diverge (B, fig. 7) and progress towards the labellum margin. Within these, further loops may develop, concentric with the first, diverging marginally. Within these again in a small number of cases another pair may develop and follow the same path. As the outer loop approaches the margin, pigmentation generally becomes less intense, or, alternatively, the flow-line becomes dissociated into a succession of dots or short bars adhering to the original contour.

Finally, in those individuals where the line of pigment has progressed to the point of maximum incision, dots or circles of colour are thrown off in the lobal extremities. Upon this basic pattern irregularities may be superimposed: bilateral asymmetry destroys the superficial balance, and random dissociation into dots and short bars makes it difficult for the eye to grasp an underlying organisation.

The system in *O. Fuchsii* and *O. ericetorum* is fundamentally the same when viewed in relation to the venation of the labellum in the two species. In the former, there is a marked angular divergence between those veins which run out into the lateral lobes and those which pass into the median lobe; in the latter the divergence between individual veins is roughly constant from margin to margin (fig. 6). Since the pigment lines are oriented, at least marginally, approximately normally to the veins, there is thus a much more marked divergence in the loops in *O. Fuchsii* than in *ericetorum*. Even so, the majority of individuals of *ericetorum* reveal the dual nature of the loop pattern. The characteristic peppered appearance of the labellum in the latter species apparently arises from a tendency for the pigment lines to break up into short segments at an early stage.

HYBRIDITY.

A considerable number of hybrid forms was observed in Hebridean Dactylorchid colonies during 1947. In the following list the determination of those starred was confirmed from fresh specimens by the late Mr. H. W. Pugsley. The type of habitat is indicated after each locality as follows: (V) Virgin ground, at the most influenced only by light grazing; (G) Heavily grazed, or cut for

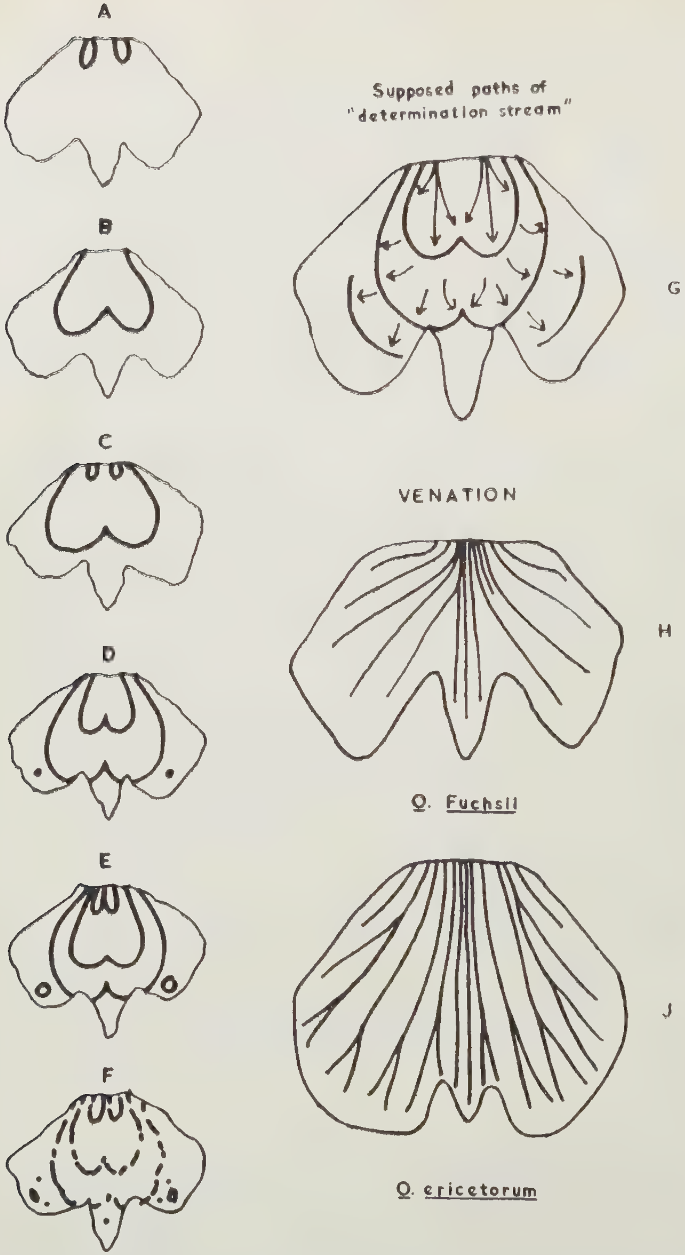
A
B
C
D
E
F
Supposed paths of
"determination stream"
G
VENATION
H
O. Fuchsii
J
O. ericetorum

Fig. 6.—Illustrating the concept of "flow-lines" as a basis for labellum patterning in *Orchis*. A–F: recognisable stages in the generation and divergence of pigment determination streams. G: paths of determination stream interpreted in relation to labellum venation. H, J: typical patterns of venation in *O. Fuchsii* and *O. ericetorum*. Explanation in text.

hay; (D) Disturbed ground: pathways, drains, fallowed fields, etc.

**Orchis Fuchsii* var. *hebridensis* × *latifolia.*

Coll: Two plants at Bousd (G), one at Grishipoll (V), three or more at Sorisdale (V).

Barra: Two plants near Loch St. Clair (V).

**O. Fuchsii* var. *hebridensis* × *purpurella.*

Coll: Hybrid colony at Arinagour (D), two or three plants at Sorisdale (V), two plants at Clabhach (G).

Barra: Large hybrid colony at Glenlots, near Castlebay (D), two or three plants near Loch St. Clair (V).

O. Fuchsii var. *hebridensis* × *ericetorum.*

Odd plants suggesting this parentage were located on Coll, Tiree, and Barra, generally growing in the ecotone between machair and moorland. Two large hybrid colonies occur on Tiree between Gott Manse and Dun an t-Sithein, and are considered further below.

**O. Fuchsii* var. *hebridensis* × *Gymnadenia conopsea.*

Coll: Two plants at Ballyhaugh (V), three or more between A Croic and Cornaig Beg (V).

**O. Fuchsii* var. *hebridensis* × *Coeloglossum viride.*

Coll: One plant of this unusual hybrid was located near Breachacha (G).

O. ericetorum × *latifolia.*

Coll: ? Two plants between Breachacha and Roundhouse (G).

O. latifolia × *purpurella.*

Barra: One or two plants near Loch St. Clair (V).

In general, where large numbers of hybrid individuals occur mixed with the pure species, or where mongrel colonies of the nature of "hybrid swarms" have arisen, it is true to say that the area concerned has suffered recent disturbance either by drainage or through other operations of agriculture. This is in accord with findings of many who have examined hybrid orchid colonies, and is remarked upon by Pettersson (1947) in a recent description of *Orchis incarnata* (*O. latifolia* L. sec. Pugsl.) × *maculata* (a form near *O. Fuchsii* Druce according to Mr. Pettersson *in litt.*).

Hybrids are not entirely absent from undisturbed areas, but are generally represented by one or two individuals, so intermediate in character as to suggest that they are exclusively an F 1 progeny. In view of the obvious interfertility which exists between the species, it is perhaps surprising that hybridity is not more frequent in these natural areas, particularly between those forms whose range of soil preferences adjoin or overlap (see fig. 7). In part, this is to be attributed to the fact that the movements of pollinating insects are remarkably restricted, machair and moor each having its exclusive group of pollen vectors. In addition, of course, any slight lack of vigour in hybrid progeny would tend to make their colonisation of closed native communities difficult, a check which would be less effective in virgin ground opened up by human activity.

Two of the "swarm"-forming hybrids are of special interest taxonomically, and also because they apparently demonstrate unrestricted fertility between plants of different chromosome groups. These are the *O. Fuchsii* var. *hebridensis* × *purpurella* swarms of Coll and Barra, and the *O. Fuchsii* var. *hebridensis* × *ericetorum* swarms of Tiree.

A considerable colony of the former hybrid occupies a stretch of waste ground by the Castlebay-Northbay road, between Castlebay and Glenlots, Barra. The parent species are abundant in the vicinity: *O. Fuchsii* bordering cultivated fields, and *O. purpurella* alongside the stream which runs into the sea at Glenlots. The characters of twenty-four individuals gathered at random from the colony are listed in Table X. The extreme diversity is obvious. Perhaps more important than the mere re-combination of characters involved, or the appearance of intermediacy in such features as colour, sepal posture, stem hollowness, and spur shape, is the fact that *qualitatively* different and new characters are apparently being synthesised. For example, neither parent, pure, exhibits ring-spotted leaves, while several of the hybrid forms show ring spotting of varying degrees of intensity. Further, many of the segregates exhibit considerable elaboration of lateral sepal pattern beyond anything encountered in parental types.

This development recalls the synthesis of new characters obtained by Baur in *Antirrhinum* hybrids (Baur, 1932), and is probably similarly attributable to the constitution of new gene patterns involving contributions from each parent. The taxonomic significance is obvious.

In the large hybrid swarms of *O. Fuchsii* × *ericetorum* near Scarinish, Tiree, there is no evidence of character synthesis. The hybrids merely express varying degrees of intermediacy between the neighbouring parental forms. The colonies occur on pastures reclaimed by drainage from *Calluna* heath.

TABLE X.

SEGREGATION OF TAXONOMIC CHARACTERS IN TWENTY-FOUR INDIVIDUALS OF AN O. FUCHSII × PURPURELLA HYBRID SWARM. THE ORDER FROM 1 TO 24 IS THAT OF DECREASING INTENSITY OF LABELLUM COLOUR.

Plant No.	Stature (cm. Classes).	Leaf Marking.	Stem.	Labellum Colour.	Labellum Shape.	Labellum Pattern.	Sepal Posture.	Sepal Pattern.	Spur Shape.	Number of Flowers.
1	28	Nil	H	1	DL	U	E	MS	BBlL	28
2	23	Nil	H	1	U	U	D	Nil	BBlS	19
3	22	Nil	PH	1	U	D	E	FL	BBlS	17
4	22	Nil	H	2	IL	U	HE	FS	BPL	18
5	31	HB & Bl	S	2	IL	D	D	L	NPL	47
6	22	Nil	H	2	IL	U	HE	MS	BPS	15
7	21	B & HB	S	3	U	U	E	ML	BPL	27
8	23	Nil	PH	3	DL	E	E	ML	NPL	12
9	30	R & B	H	4	IL	D	HE	FS	BBlL	26
10	24	L	S	4	DL	D	E	FS	BPL	17
11	23	B	H	5	IL	C	D	FL	BPS	14
12	21	B & Bl	S	5	DL	E	HE	LS	BBlL	30
13	20	Nil	H	5	U	D	E	MS	BBlS	24
14	21	L	H	6	IL	B	D	S & L	NPS	12
15	28	HB & R	S	6	ML	D	E	Nil	NPS	25
16	18	L & B	H	7	IL	U	D	S	BBlL	15
17	28	Nil	H	7	U	E	E	FS	BBlL	44
18	18	HB & Bl	S	7	ML	D	D	Nil	NBlS	29
19	24	H	S	7	ML	F	E	HL	BBlS	31
20	28	HR	S	7	IL	D	HE	S & L	BPL	12
21	27	R	S	7	IL	C	E	S	BBlL	12
22	22	HB & Bl	H	8	IL	D	E	L	NPL	20
23	24	R	H	8	DL	U	E	L	BPL	37
24	23	L	H	8	IL	E	E	S & L	BBlS	26

CODE.—Leaf: L=light dotting; H=heavy spotting; Bl=heavy blotches; B=bars; HB=heavy bars; R=pigmented rings; HR=heavily pigmented rings.
Stem: S=solid; PH=small cavity; H=hollow.
Labellum colour: Grades as in fig. 1.
Labellum pattern: Stages as in fig. 6.
Labellum shape: U=unlobed; IL=indistinctly 3-lobed; DL=distinctly 3-lobed; ML=very markedly 3-lobed.
Sepal posture: E=erect; HE=half erect; D=drooping.
Sepal pattern: S=spotted; L=lined; H=heavy; M=medium; F=faint.
Spur shape: B=broad; N=narrow; P=pointed; Bl=blunt; S=short; L=long.

Discussion.

Ecological Inter-relationships.

Fig. 7 is a presentation in summary form of fifty-eight determinations of soil-pH in as many colonies of Dactylorchids in the islands of Coll, Tiree, Barra, and South Uist. The closeness with which each form adheres to its own particular range of soils is emphatically expressed, serving to bear out factually what is perfectly clear to an observer in the field. The ecological communities to which the various forms belong are in turn related in their hierarchy of species to these varying degrees of soil acidity (Tables I and II), and reflect further the varying requirements of the orchid forms for soil moisture.

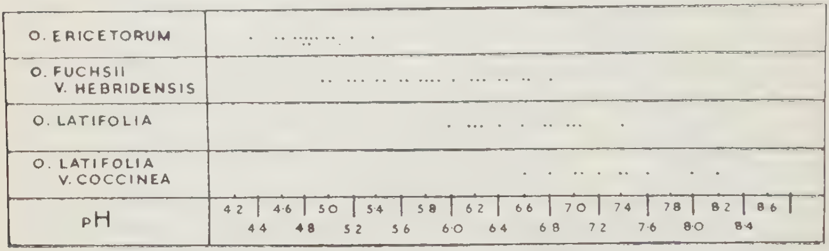

Fig. 7.—Correlation of Dactylorchid species and habitat soil-pH. Fifty-eight determinations, Coll, Tiree, Barra, and South Uist.

O. ericetorum is a plant of moist peat moor, definitely acid in reaction. While frequently found growing in Sphagnum, it is not really a plant of saturated peat *bog*, and is in fact entirely absent from blanket-bog where that formation is developed. *O. Fuchsii* var. *hebridensis* characterises moist, but again not saturated, meadow-land and pasture, a good deal less acid in reaction. This preference makes it by far the most common orchid of areas of cultivation. *O. latifolia* L. sec. Pugsl. is, on the other hand, definitely a species of wet marshland, still less acid in reaction. The var. *coccinea* is restricted to calcareous duneland, and is usually to be found in dune slacks. It seems tolerant of a much greater degree of desiccation than the type.

The least abundant of the marsh orchids in these islands is *O. purpurella*. On Coll it overlaps with *O. Fuchsii* var. *hebridensis* at Arinagour and Breachacha in meadow-land of pH 6·0–6·2, and with *O. latifolia* around Loch Cliad and at Sorisdale in marshland, pH 6·6–6·8. Similarly on Barra it occurs with *O. Fuchsii* around Castlebay in soils pH 6·4–6·6, where it forms the hybrid swarm described in a previous section. Around Loch St. Clair on the same island, in marshland near neutral in reaction, it accompanies, and hybridises with, *O. latifolia*.

The ecological preferences of the various forms leads to a pattern of distribution which is likely to deceive the cursory observer. On Barra, for example, the impression gained from roads and areas of habitation is that *O. Fuchsii* var. *hebridensis* is overwhelmingly the most abundant orchid. Notwithstanding the much thinner distribution on moorland of *O. ericetorum*, the latter is, however, undoubtedly present in greater numbers on the island as a whole.

The Pattern of Variation.

Without large scale and prolonged experimental studies it is, of course, impossible to define with any precision the degree to which the variation encountered is due to environmental as apart from genetical causes. Much of the variation in plant stature is apparently environmentally controlled, and a correlation is usually evident with the height of neighbouring vegetation. The large difference between the *O. Fuchsii* var. *hebridensis* of the Tiree Iris-bed population T. II and adjoining meadow-land colonies is a case in point. The stature difference between populations of *O. latifolia* and *latifolia* var. *coccinea* appears, on the other hand, to be genetically determined. Throughout the range of the two forms, a height ratio of practically 2 : 1 in population means is maintained. The relative dwarfness of the variety *coccinea* was noted in the original diagnosis of Pugsley—"*Planta vulgo satis nana*" (1935).

Intra-population variability in floral and foliar characteristics is somewhat more marked in the *maculata* complex than in *O. latifolia* and varieties. There is no evidence to suggest that this intense variation is dependent upon the operation of gross environmental factors; on the coast and inland, in lush meadow-land and thin pasture, a similar type and range of variability is encountered. Among the floral characteristics this can be said of pattern, shape, and, in general, of colour, although the slight shift of population colour mean for the Tiree Iris-bed colony of *O. Fuchsii* var. *hebridensis* may indicate loss of intensity due to excessive shading.

The outstanding feature of the floral variation is its continuity: for each form there is a remarkably smooth intergradation from extreme to extreme centred around the population mean. Labellum shape, colour, and, as has been seen, pattern vary independently in the same manner. Such variability, of course, is by no means peculiar to Hebridean colonies: in floral and certain foliar characters the Dactylorchids are among the most variable of British plants. In the absence of experimental genetical data any explanation of this condition must remain largely hypothetical. If it is the outcome of random distribution of numerous allelomorphic genes, then the situation could conceivably have arisen as the result of former hybridity. We have as examples of such a process the hybrid swarms mentioned in a previous section which have arisen between normally isolated species where ecological barriers have been artificially upset. However, the very fact that similar variability occurs in isolated populations over so wide an area makes it improbable that diversification has arisen as the result of *recent* hybridity. Restricting the discussion to the Hebridean colonies analysed above, if it is supposed on the other hand that the present island populations of *O. Fuchsii*, for example, are the isolated remnants of an ancient continuous mongrel population, the picture becomes somewhat more convincing. The question then arises: why, in the period succeeding isolation, have the colonies failed to achieve stability? Ecologically, stability has been attained, and *O. Fuchsii* var. *hebridensis*, like the other native Dactylorchid forms, occupies a precise position in the biota of the various islands. The persistence of extreme floral variability remains a problem. To the student versed in the lore of mathematical population mechanics, it may seem inconceivable that a race should persist as long as this, in presumably panmictic populations of varying size isolated by secular barriers, without some "decay of variability" making itself apparent. According to the orthodox doctrine, this should occur either through the agency of "natural selection," or through the operation of the purely mechanical principles, variously enunciated by Fisher and Sewall Wright, which, in the words of Dobzhansky (1941), bring about a situation where "a finite population left to its own devices must . . . suffer a progressive decay of its hereditary variability and sooner or later must reach a complete genetic uniformity."

Alternatively, the variability of orchis flower characters could be attributed to the existence of recurrently mutating "floral" genes (the plural is necessary if the facts of independent variation are to be explained). Again, in the absence of experimental evidence, the view seems quite tenable. It does not, however, explain why isolated populations should come to possess the same structure of variability *irrespective of size.* It may presumably be argued that the apparent population sizes in no way reflect the actual extent of panmictic units, and that, genetically, the dense *O. Fuchsii* var. *hebridensis* colonies of the west of Barra break up into breeding units comparable with those of the west of South Uist, where the species is much more diffuse.

In the above discussion emphasis has been placed upon the broad similarity in range of variability that exists in the forms of the *maculata* complex over the area considered. However, while the sweep of variation is similar, there is some evidence of geographical race differentiation, expressed in the alteration of the position of population means for certain characters from island to island. Thus, as has been indicated, the Barra and South Uist version of *O. Fuchsii* var. *hebridensis* differs in the characters of leaf marking and labellum shape from the version of the variety found on Coll and Tiree. Presuming common ancestry, this would suggest slight divergence subsequent to the development of the geographic barriers, unaccompanied by any reduction in inherent variability.

Taxonomy.

Regarded from the point of view of orthodox taxonomy, the groupings set forth in the introductory paragraphs cover the Dactylorchids considered in the present study with the addition of the new subspecies, *O. Fuchsii* subsp. *rhoumensis*. There is rarely any difficulty in recognising the affinities of pure *populations*, or in deducing the parentage of populations of putative hybrids. It will be clear from the variation curves, however, that in dealing with *individuals* it is possible to find variants with one or more characters suggesting intermediacy. Further, plants may be found in a colony of *O. Fuchsii*, for example, with the entire complex of characters similar to extreme variants of *ericetorum*. Nevertheless, these are the comprehensible results of the broad systems of morphological variation existing in the group; the position of "specific," "subspecific," and "varietal" foci remain quite clear, and the reality of the major groupings remains unimpaired.

The problem of the *rank* to be accorded to these various groupings is somewhat more involved. The Dactylorchids are one more example of a complex of plants in which the separation of taxonomic units is largely based upon quantitative differences, and in which the outline of such units is locally "blurred" by the occurrence of hybridity. Two cytological series exist among the Hebridean forms here considered: a diploid in which $2n = 40$, and tetraploid in which $2n = 80$. The series are as follows:—

Diploid ($2n = 40$).	Tetraploid ($2n = 80$).
O. Fuchsii: With var. *hebridensis* and subsp. *rhoumensis.*	*O. ericetorum.*
O. latifolia: With var. *coccinea.*	*O. purpurella.*

Putative hybrids between various combinations of these forms have been recorded in the Hebrides in the present paper and in publications of Campbell (1937), Wilmott (1939), and J. W. Heslop Harrison (1941). Similarly, hybrids between various combinations of the mainland versions of *Fuchsii*, *ericetorum*, *latifolia*, and *purpurella* have been recorded elsewhere in Britain on occasions too frequent to enumerate. Hybrid "*swarms*," that is, colonies where a majority of individuals are of presumed hybrid origin, are almost equally well represented in the literature. Special interest attaches to those which are attributed to hybridity between parents belonging to the different chromosome groups. Such are the *O. Fuchsii* var. *hebridensis* × *ericetorum* and *O. Fuchsii* var. *hebridensis* × *purpurella* colonies recorded here from Barra, Coll, and Tiree. A similar swarm near Birtley, Co. Durham, has been under observation by the writer for three seasons. Here again there is remarkably little apparent reduction in seed fertility, and clearly F 1 chromosome behaviour should be of considerable interest; this is at present under investigation.

The inadvisability of placing too much weight upon the evidence of putative hybrids has been well expressed recently by Baker (1947). Nevertheless, accepting the available facts at their face value in the present absence of information about the fertility of hybrids produced under controlled experimental conditions, it seems that such sterility barriers as there are present in the sub-genus do not effectively check gene exchange when the species come intimately into contact. Further, it is evident that ecological factors are of great importance in maintaining the independence of the various forms, firstly through bringing about spatial separation, and secondly by discouraging the establishment of hybrid races.

If this is indeed the case, then the sub-genus becomes one coenospecies in the terminology of Turesson; the "species" emerge as ecospecies, and certain of the subspecific units as morphologically marked ecotypes.

It is proposed to adduce additional evidence in support of such a view of the Dactylorchids in a further communication.

SUMMARY.

1. The distribution of Dactylorchid populations on the islands of Coll, Tiree, Rhum, Barra, and South Uist in the Inner and Outer Hebrides shows that a close correlation exists between edaphic factors and the form occurring.

2. Biometrical analysis of certain taxonomic features reveals that there is a slight divergence between the populations of *Orchis Fuchsii* var. *hebridensis* of the Inner Hebrides and those of the outer group of islands. No such race divergence is apparent in *O. ericetorum* or in the *latifolia* forms within the area so far covered.

3. An orchid with a diploid chromosome number of 40 and many characters of intermediacy between *O. Fuchsii* and *O. ericetorum*, here named *O. Fuchsii* Druce subsp. *rhoumensis* H.-Harr. f., exists on the Isle of Rhum.

4. The significance of the excessive variability of many foliar and floral characters in the Dactylorchids is discussed, and a basis for the interpretation of the range of labellum patterning occurring in the *maculata* complex is proposed.

5. The extreme interfertility which exists between Dactylorchid forms, and the degree to which the maintenance of their taxonomic independence rests upon ecological isolation, suggests that the subgenus should be regarded as a single coenospecies in the terminology of Turesson.

ACKNOWLEDGMENTS.

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EXPLANATION OF PLATES.

PLATE I.

Photo. 1. *Orchis Fuchsii* var. *hebridensis*. Unselected group of mounted lips from the Barra colony, B. II. (Approx. natural size.)

Photo. 2. *Orchis Fuchsii* var. *hebridensis*. Unselected group of mounted lips from the Tiree colony, T. II. (Approx. natural size.)

PLATE II.

Photo. 1. *Orchis Fuchsii* subsp. *rhoumensis*. Unselected group of mounted lips from Harris, Isle of Rhum. (Approx. natural size.)

Photo. 2. *Orchis Fuchsii* var. *hebridensis*. Unselected group of mounted lips from the Tiree colony, T. III. (Approx. natural size.)

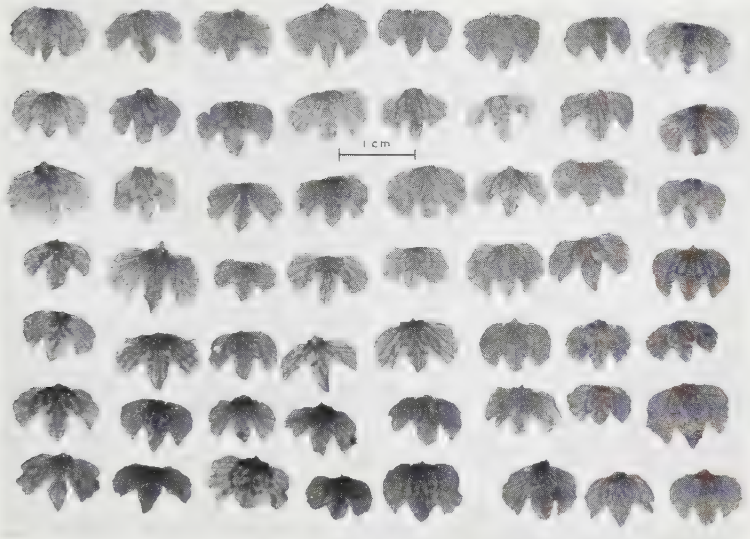


Photo. 1.

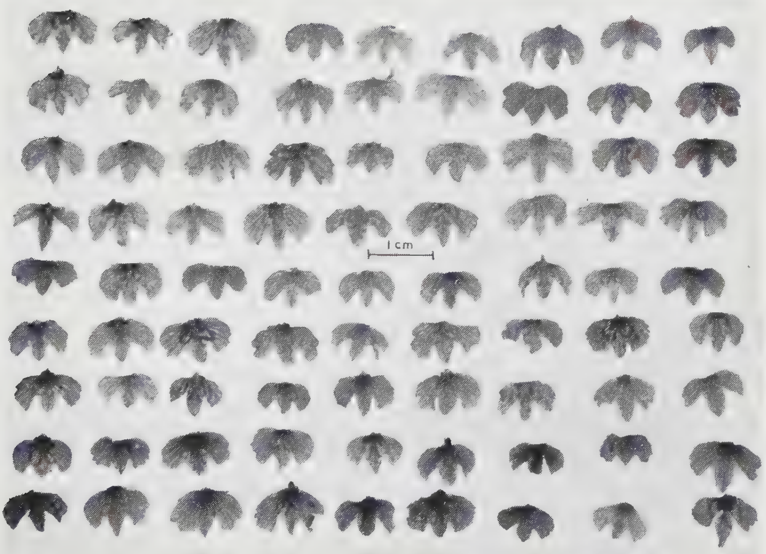
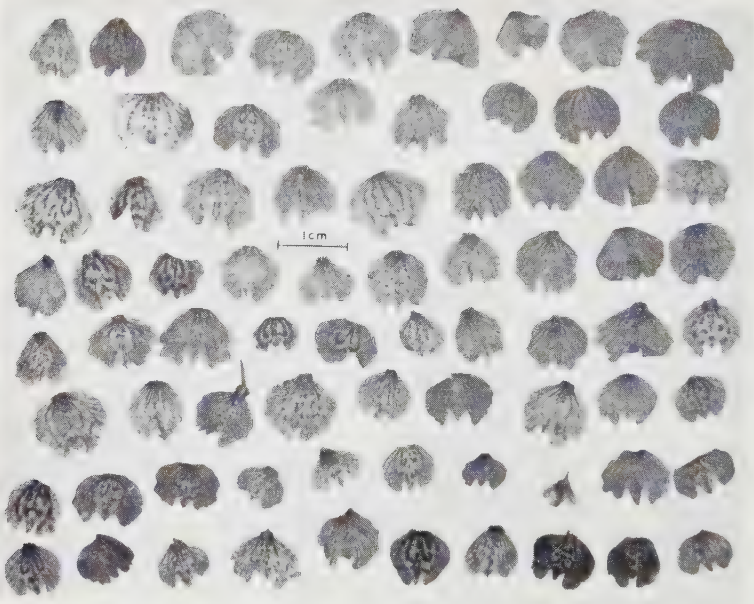


Photo. 2.

J. Heslop Harrison.



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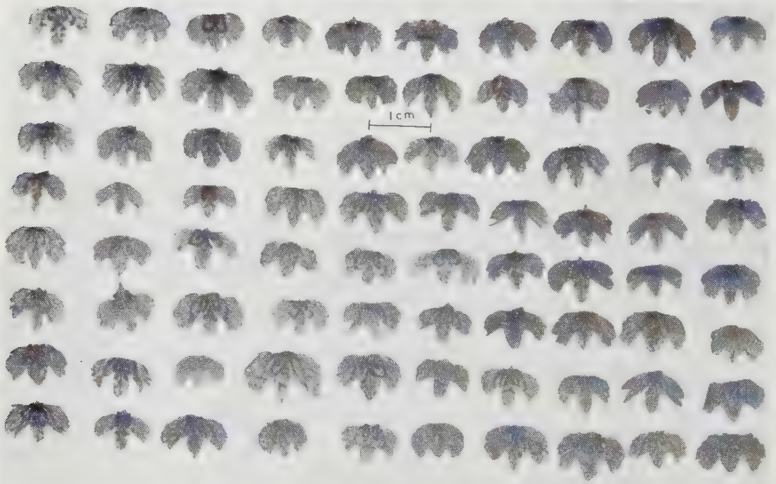

Photo. 2.

J. Heslop Harrison.

SOME ASPECTS OF THE PLANT ECOLOGY OF THE ISLAND OF BARRA.

By ANNA M. MACLEOD, B.Sc. (With Two Maps.)

(Read 15th January 1948.)

INTRODUCTION.

The island of Barra is the most southerly of the five main Hebridean Islands, which form a chain off the west coast of Scotland. In 1936 a preliminary account of the natural history of Barra was published by members of the Edinburgh University Biological Society (Forrest, Waterston and Watson, 1936), and since that date the records of species have been amplified by various workers (Harrison, 1941; Watson, 1939; Wilmott, 1939). This present paper deals with the development and relationships of the various plant communities found on the island, and the lists of species of different associations are nowhere intended to be exhaustive.

The climate of Barra is characterised by mild winters and cool summers, the January isotherm of 42° F. passing east of Barra, and the July isotherm of 56° F. skirting its northern coast. Precipitation is high, 40 inches of rain being the mean annual figure for the years 1906–35 (Stamp, 1941). The prevailing wind is from the south-west, and gales in winter and at the equinoxes are common. These gales drive considerable quantities of calcareous sand on to the western aspects of the island up to a height of over 300 feet.

The rocks of Barra are mainly gneiss, and bare stones frequently protrude through the blanket of peat which covers most of the interior. There is evidence of glaciation over the whole of the island, and perched blocks are everywhere common. There are no raised beaches, but, on the contrary, the islands in Bay Hirivagh and the levels of some of the lochs suggest subsidence (Jehu and Craig, 1921–25).

VEGETATION.

A. *Moorland.*

Most of the interior of Barra is covered by heather moor or grass moor, or by a mixed heather-grass moor (Map 1). Both the pure and the mixed moors are underlaid by peat, which varies in depth from 1 foot to over 10 feet. As a result of regular cutting of peat for fuel the vegetation is not uniform, but represents different stages in a seral succession leading to the climatic climax of moorland dominated by *Calluna vulgaris* * or by *Scirpus caespitosus.*

(1) *Pure Heather Moor.*—This association is dominant on the southern half of the peninsula of Bruernish, on Ard Rudha and in the upper reaches of Glen Dhu. The peat in all these regions has a pH of approximately 4·4.

In Bruernish and on Ard Rudha, where the heather is regularly burned at intervals of fifteen years, the Callunetum is of two different types. Burning is not severe, and the fresh growth produces an even sward dominated by *Calluna vulgaris. Deschampsia flexuosa* is frequent among this short heather, and *Molinia caerulea, Potentilla erecta, Anthoxanthum odoratum* and *Carex binervis* are all occasional. As the *Calluna* ages, growth becomes more tussocky and the constituents of the ground vegetation are more varied. At this stage, in addition to the above-listed species, *Blechnum spicant, Carex echinata, Festuca ovina* and *Erica cinerea* appear occasionally.

In Glen Dhu the Callunetum is much sparser in species. Patches which have not suffered from peat cutting show *Calluna vulgaris* growing to a height of 18 inches and mixed only with *Molinia caerulea* (a) † and *Potentilla erecta* (r). Near the head of the pass at an altitude of 500 feet, the composition of the Callunetum alters. The following are the main species present in this region: *Calluna vulgaris* (d), *Molinia caerulea* (o–f), *Potentilla erecta* (f), *Erica tetralix* (f), *Scirpus caesposus* (f), *Nardus stricta* (r), *Hylocomium squarrosum*, *Campylopus* spp., *Hypnum cupressiforme.* This represents the beginning of a transition to the Nardetum-Scirpetum caespitosae prevalent on the west side of Am Bealach.

In both Bruernish and Glen Dhu *Sphagnum* bogs are formed in the hollows. In Bruernish a typical *Sphagnum* bog supports the following species: *Sphagnum* spp. (a), *Scirpus caespitosus* (f), *Juncus bulbosus* (o), *Pinguicula vulgaris* (r), *Drosera rotundifolia* (r), *Molinia caerulea* (r), *Campylopus* spp. In Glen Dhu the same species are present in the same frequencies, with the exception of *Molinia*, which is abundant. Moreover, in Glen Dhu, *Narthecium ossifragum* is present (o), and *Polygala oxyptera* and *Erica tetralix* are (r).

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* *Nomenclature throughout is in accordance with the British Ecological Society's Check List of British Vascular Plants.*

† (d) = dominant; (a) = abundant; (f) = frequent; (o) = occasional; (r) = rare.

(2) *Peat Cuttings.*—Where peat has been cut, extensive changes have taken place. At the base of each cutting trenches are formed in which water accumulates, and into which are thrown the top layers of peats containing heather plants. The changes taking place in these trenches follow a regular order. Table I shows the succession in a period reputed (on local evidence) to be twenty years.

TABLE I.

SUCCESSION IN PEAT CUTTINGS IN GLEN DHU.

	Two Years.	Five Years.	Twenty Years.
Sphagnum spp.	a	o	..
Eriophorum angustifolium	f	o	..
Juncus bulbosus	f	r	..
Molinia caerulea	f	f	o
Narthecium ossifragum	r	..	..
Drosera rotundifolia	r	..	..
Carex flava agg.	r	o	..
Potentilla erecta	r	o	r
Calluna vulgaris	..	a	d
Erica tetralix	..	r	..
Anthoxanthum odoratum	..	o	r
Deschampsia flexuosa	..	r	o

At the base of a newly opened peat cutting no vegetation is present, and the trench is filled with a sludge-like mixture of peat and water, which is frequently colonised by *Potamogeton polygonifolius.* The next, and in some cases the first, invaders are species of *Sphagnum*, closely followed by *Eriophorum* and *Juncus bulbosus.* As the trench dries—and the rate of drying varies according to the drainage and the precipitation—*Sphagnum* and *Eriophorum* gradually disappear, giving place to sedges, grasses, and finally to *Calluna.* The appearance of the trench at this last stage is very uneven as a result of the accumulation of peats from the top of the cutting. In some cases the presence of large turfs with viable roots of *Calluna* explains the early invasion of heather into an unusually damp habitat. In the final stages of regeneration, when *Sphagnum* and *Eriophorum* have disappeared, the trench is as dry as the surface of the moor above it, and is filled with vegetation indistinguishable from that of the general untouched heather moor.

In the peat-cutting areas of Bruernish, as regeneration proceeds, the face of the cutting is occasionally invaded by *Rumex* spp., principally *R. acetosella*, and on several old cuttings the whole peat face is dry and cracked and covered with this species. This invasion by *Rumex* is also found near Loch nam Faoileann, but was not observed in Glen Dhu.

(3) *Mixed Moor*.—Near Loch nam Faoileann, where drainage is poor, large areas of the moor are covered by a mixed Callunetum-Scirpetum caespitosae. In the well-drained parts of the moor *Calluna vulgaris* is (a), *Erica tetralix* and *Molinia caerulea are* (f), while *Scirpus caespitosus*, *Erica cinerea*, *Nardus stricta*, *Potentilla erecta*, *Carex flava* agg., *Carex echinata*, *Eriophorum angustifolium* are (o). In the poorly drained regions *Calluna vulgaris* and *Erica tetralix* are only (o), and in tussocks, *Scirpus caespitosus* is (a), *Eriophorum angustifolium* is (f), while the other species listed above are (r). *Sphagnum* and *Narthecium ossifragum* are also (f) in the poorly drained patches.

At the present time, therefore, it seems that rapid deposition of peat, as demonstrated by the presence of the two main peat-formers, *Sphagnum* and *Eriophorum*, is taking place in two ways. First, and most generally in the drier areas, the trenches at the base of the peat-cuttings are invaded for a limited time by these peat-formers. This raises the level of the peat in the cutting, and partially fills the trench. Secondly, on the badly drained areas, especially near the lochs, *Sphagnum* and *Eriophorum* persist, forming a blanket bog, and although *Calluna* may invade to a certain extent, it does not oust the two former species.

(4) *Grass Moor—Nardetum*.—The remainder of the interior of the island is covered with grass moor, almost free from *Calluna*. This association extends over all the slopes of Heaval and most of Hartaval, and is grazed by sheep and horses. There is no record of this region ever having been dominated by *Calluna*, and it may be that its proximity to Castlebay, with consequent heavy grazing, has caused the disappearance of *Calluna* centuries ago.

The southern slopes of Heaval are covered by shallow peat (average depth 12 inches), which is less acid than that of the heather-covered hill of Bruernish. The pH varies from 4·9 to 5·3. *Nardus stricta*, *Molinia caerulea* and *Festuca ovina* are all (f); *Sieglingia decumbens*, *Juncus articulatus*, *Euphrasia officinalis* agg., *Carex echinata*, *Prunella vulgaris*, *Plantago lanceolata*, *Thymus serpyllum* agg. and *Potentilla erecta* are (o); while *Anthoxanthum odoratum*, *Calluna vulgaris* and *Campanula rotundifolia* are (r). Less well-drained areas of the Nardetum support *Scirpus caespitosus*, *Pedicularis palustris* and *Eriophorum angustifolium*, but as a result of the angle of slope of the hill such marshy patches are not common.

In the north of Bruernish a grass moor is formed on deeper, more acid peat (pH 4·5). The same grasses are present as on Heaval, but in addition *Scirpus caespitosus* is abundant and *Holcus lanatus* occasional.

A number of lochs are present in the moorland. The ecology of these lochs has already been fully dealt with (Forrest, Waterston and Watson, 1938) and is not further discussed in this paper.

B. *Seashore Associations.*

Three different types of seashore association are found round the coast of Barra: salt-marsh, cliff, and sand-dune associations. The first two present no features of especial interest, and are neither extensive nor rich in species.

Sand-dunes.—On the strand below the dunes the flora is rather restricted. *Cakile maritima*, *Senecio jacobaea*, *Rumex crispus*, *Atriplex glabriuscula*, and *Lotus corniculatus* are all present on most of the beaches, but are nowhere abundant.

The stages in the stabilisation of sand-dunes are similar in all parts of the island.

Stage A. Unfixed Dunes.—These are colonised only by *Ammophila arenaria*, and are subjected to inundations of blown sand at frequent intervals.

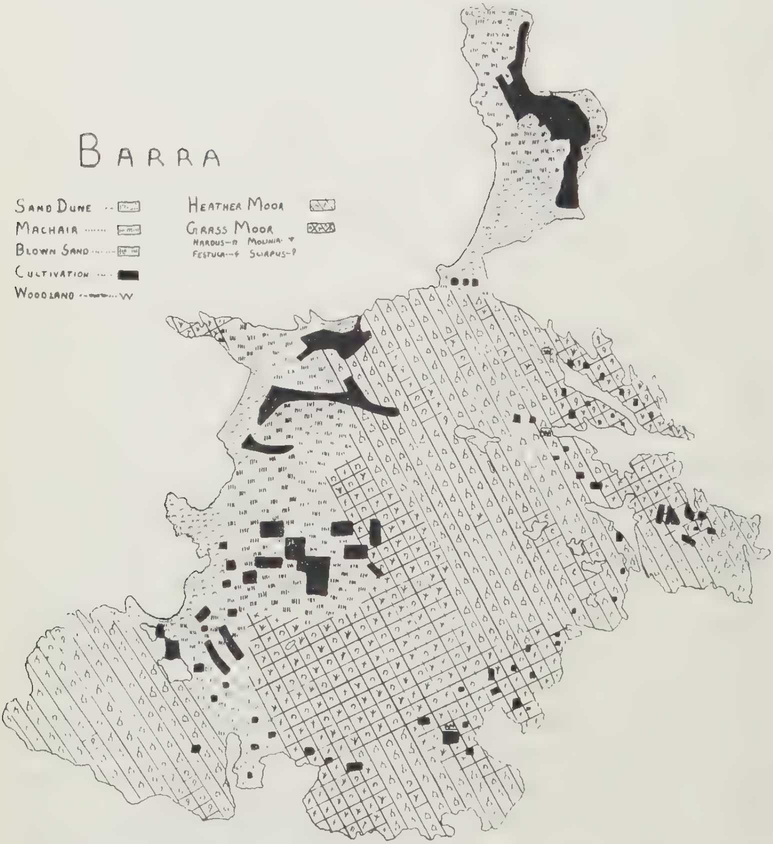
Stage B. The first species colonising the *Ammophila*-covered dunes are normally *Senecio jacobaea* and *Tussilago farfara* (r), with *Agropyron junceum* and *Ranunculus acris* (v.r.). This is not a stable association, as at this stage again sand is liable to drift over and submerge the vegetation. Further inland, when exceptionally heavy drifts of sand cover the machair, the shoots of *Senecio jacobaea* and *Ranunculus acris* are again the first to penetrate the cover.

Stage C. A few yards beyond the crest of the dunes, while *Ammophila* is still dominant, other species obtain a foothold on the now more stable sand. *Galium verum*, *Trifolium repens*, *Achillea millefolium*, *Festuca rubra*, *Plantago lanceolata*, *Carex arenaria* and *Erodium cicutarium* agg. are all (o) at this stage.

Stage D. In the lee of the dunes *Ammophila* has greatly decreased, *Carex arenaria* and *Agropyron junceum* have disappeared, and the Dicots in *C*, with the exception of *Tussilago farfara*, have become more frequent. *Bellis perennis* and *Cerastium vulgatum* are here (o). Mosses, such as *Tortula ruraliformis* and *Hylocomium squarrosum*, are noticeable on all bare patches.

Stage E. One hundred yards from the sea the vegetation has become stabilised. *Ammophila* is absent, the Dicots in *C* and *D* are present in much the same frequencies as before, *Trifolium repens* has increased in frequency, and grasses, such as *Lolium perenne*, *Agrostis stolonifera*, *Holcus lanatus* and *Poa pratensis* agg., are beginning to assume greater prominence in the composition of the sward. There are no bare patches and few mosses. This machair, or sea-meadow, which is grazed by cattle, covers all the isthmus from Traigh Eais to Ben Eoligarry. The abundance and luxuriant growth of Dicots, and of leguminous plants in particular, gives the machair in summer a characteristic smell and brilliant appearance.

MAP I: VEGETATION


BARRA
SAND DUNE
MACHAIR
BLOWN SAND
CULTIVATION
WOODLAND
HEATHER MOOR
GRASS MOOR
NARDUS—n MOLINIA—▼
FESTUCA—f SCIRPUS—?

The distribution of machair is shown in Map 1, and while the individual species vary in frequency, the general appearance is similar in all districts. Some of the areas analysed are tabulated below. Species which in no case achieve a higher frequency than (r) have been omitted.

TABLE II.

MACHAIR ANALYSIS.

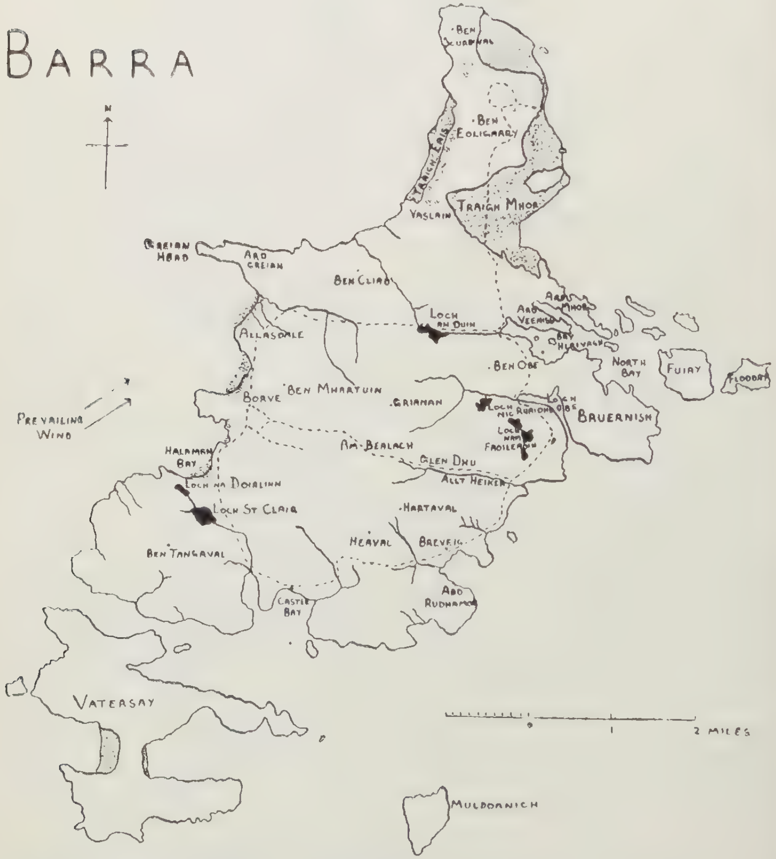
	Halaman Bay.	Borve.	Loch St. Clair.
Anthyllis vulneraria	a	o	..
Trifolium medium	a	..	f
Euphrasia officinalis agg.	a	o	o
Galium verum	a	o	f
Plantago lanceolata	f	f	f
Festuca rubra	f	f	f
Bellis perennis	o–f	f	o
Heracleum sphondylium	o	r	o
Trifolium repens	o	o	o
Cerastium vulgatum	o	o	..
Viola curtisii	o	r	o
Erodium cicutarium agg.	o	r	r
Senecio jacobaea	o	f	o
Vicia cracca	o	..	o
Thalictrum arenarium	o	..	r
Lotus corniculatus	o	f	o
Prunella vulgaris	o	..	..
Achillea millefolium	o	f	..
Poa pratensis	o	o	o
Taraxacum officinale	r	..	o
Lolium perenne	r	o	f
Daucus carota	r	o	o
Hieraceum pilosella agg.	..	o	..
Centaurea nigra	..	r	o
Rhinanthus minor agg.	..	r	o
Poa annua	..	r	o

C. *Influence of Blown Sand.*

Blown sand has a considerable influence on the vegetation of the west coast of Barra. The effect of sand is perhaps most marked on the slopes of the two hills, Ben Eoligarry and Ben Mhartuin.

The south-western side of the base of Ben Eoligarry is covered with vegetation similar to that on the machair behind Traigh Eais, and is formed from calcareous sand over three feet deep. The pH at the surface and at a depth of one foot were both found (July 1947) to be 7·8. Apparently such leaching as had taken place had been counteracted by further accumulation of sand. (This figure varies from time to time according to the amount of driven sand and the precipitation. Data obtained in 1938 (private communication, A. S. Boughey) showed a pH of 7·8 on the surface and 8·0 at a depth of one foot.

Map II


BARRA
N
Ben Scurval
Ben Eoligarry
Traigh Eais
Traigh Mhor
Vaslain
Greian Head
Ard Greian
Ben Cliad
Loch an Duin
Ard Mhor
Ard Veenish
Bay Hirivagh
North Bay
Fuiay
Flodday
Ben Obe
Allasdale
Borve
Ben Mhartuin
Grianan
Loch nic Ruaidhe
Loch Obe
Bruernish
Loch nam Faoileann
Prevailing Wind
Halaman Bay
Am Bealach
Glen Dhu
Allt Heiker
Loch na Doirlinn
Loch St Clair
Hartaval
Heaval
Brevig
Ben Tangaval
Castle Bay
Ard Rudhamor
Vatersay
0
1
2 Miles
Muldoanich

At a height of 100 feet the soil is 4 feet in depth and is greatly interrupted by rabbit scrapes and associated bare patches. The surface pH here is 7·4, while at a depth of one foot the pH is 7·6. Again the vegetation resembles that of the machair. At 200 feet the soil is 13 inches deep with a pH of 7·0. More grasses are present at this height than lower down the hill. On the summit the soil reaches a depth of only 6 inches and is more peaty in texture, though the sand evenly mixed through makes the pH 6·5. Still more grasses are present on the summit, and among them is included *Nardus stricta*. Very short shoots of *Calluna vulgaris* are also found here. The *Primula vulgaris*, which is found at all heights on the hill, shows marked signs of iron deficiency, with yellowing from the tips and margins of the leaves. The frequencies of some of the species found on Ben Eoligarry are shown in Table III.

TABLE III.

FREQUENCIES ON BEN EOLIGARRY.

	Base.	100 feet.	200 feet.	Summit.
Galium verum . . .	f	o	o	. .
Lotus corniculatus . . .	f	o–f	o	r
Trifolium repens . . .	a	o	o	r
Plantago lanceolata . .	f	f	o	o
Ammophila arenaria . .	r	o	. .	. .
Potentilla erecta . . .	. .	. .	r	o
Calluna vulgaris . . .	. .	. .	. .	r
Nardus stricta . . .	. .	. .	. .	r

It can be seen, therefore, that sand influences the soil, and through it the vegetation, up to a height of 338 feet, and inland to a distance of over 600 yards. On the east coast of the island, where there is little sand and where the prevailing winds blow offshore, the slopes of all hills of this height (*cf*. Ben Obe) are covered with a very different type of vegetation, viz. grass moor or heather moor, interspersed with patches of bog.

On Ben Mhartuin analyses of the vegetation were made on all slopes of the hill. The west of the Ben and, to a lesser extent, the south are exposed to the south-west winds laden with sand blown from Halaman Bay, while the northern slopes are influenced by sand carried from Allasdale. On the eastern slope the ground is sheltered from the wind by the rest of the hill and shows no sand at any depth. The configuration of the landscape is physiographically rather similar to that round Loch nam Faoileann, but the areas affected by blown sand bear a very different vegetation. The eastern slopes, unaffected by sand, have a pH of 4·7 and bear a mixed *Scirpus Calluna* moor, with no trace whatsoever of calcicolous types. *Molinia caerulea* is here (a), *Nardus stricta* (o), and *Eriophorum angustifolium* (r). The other aspects of the hill are covered with a soil which is peaty in texture but impregnated with grains of sand. The pH on the west is 5·8, and on the north and south is 6·0. The vegetation contains both moorland types such as *Calluna vulgaris* and *Molinia caerulea*, and calcicolous types such as *Anthyllis vulneraria*. Grasses such as *Holcus lanatus*, *Deschampsia flexuosa*, *Festuca ovina*, *Anthoxanthum odoratum*, *Cynosurus cristatus* and *Sieglingia decumbens* constitute the major part of the vegetation on all slopes except the eastern one.

The unusual association of *Calluna* (a calcifuge) with *Anthyllis* (a calcicole) can also be observed on the roadside at Traigh Mhor. Here the shell sand used for road-making has been driven up on to the Callunetum by passing traffic and has become mixed with the peat. The pH is 6·7 instead of 4·4, as found on the moorland above, and the roots of *Calluna* and *Anthyllis* are found in the same few cubic inches of soil. Other species found on this patch of roadside include *Thymus serpyllum* agg., *Primula vulgaris*, *Anthoxanthum odoratum*, *Lotus corniculatus*, *Erica cinerea* and *Hypericum pulchrum*.

Greian Head, at the farthest west extremity of the island, also illustrates the effect of sand on vegetation. The actual headland itself lies westward beyond the influence of the sand (though it is subjected to considerable salt spray during the winter storms), but the character of the soil and the vegetation on Ard Greian are modified in varying degrees by the sand blown across from Allasdale. This is well illustrated by a comparison of two regions, each with alternating ridges and furrows, the first exposed to the blown sand, and the second too far west to be greatly affected by it. These two regions lie at the same altitude and have the same angle of slope. The vegetation on Ard Greian takes the form of sand-dunes on the ridges and machair in the hollows, while that on Greian Head is of a grass-moor type on the ridges with the beginning of bog in the hollows. The ridges of Ard Greian are thus dominated by *Ammophila arenaria*, with *Galium verum*, *Senecio jacobaea* and *Festuca rubra* (f), *Plantago lanceolata*, *Trifolium repens*, *T. medium*, *Bellis perennis* and *Alopecurus geniculatus* (o), and *Prunella vulgaris* and *Daucus carota* (r). The hollows have *Holcus lanatus*, *Cynosurus cristatus*, *Festuca rubra*, *Achillea millefolium* and *Plantago lanceolata* (f), *Lolium perenne*, *Sieglingia decumbens*, *Prunella vulgaris*, *Trifolium repens*, *T. medium*, *Bellis perennis*, *Plantago maritima*, *Galium verum* and *Anthyllis vulneraria* (o), and

Daucus carota, *Ophioglossum vulgatum* and *Coeloglossum viride* (r). The ridges on Greian Head have *Sieglingia decumbens*, *Molinia caerulea* and *Succisa pratensis* (f), *Holcus lanatus*, *Cynosurus cristatus*, *Festuca rubra*, *Prunella vulgaris*, *Carex flacca*, *Plantago maritima* and *Campanula rotundifolia* (o), and *Ranunculus repens* (r). The hollows on Greian Head differ greatly from those on Ard Greian, with vegetation showing *Juncus bulbosus* (f), *Holcus lanatus*, *Molinia caerulea*, *Poa trivialis*, *Carex flacca* and *Caltha radicans* (o), and *Cynosurus cristatus*, *Ranunculus repens* and *R. flammula* (r). The pH of the soil on Ard Greian is consistently 7·2, while that of Greian Head varies between 6·3 and 6·5.

D. *Cultivation.*

As can be seen from the vegetation map, most of the cultivated land on the island is to be found on the soils affected by blown sand, or on the edge of the machair. The valley to the east of Borve and the sandy plain near Eoligarry are the two most intensively cultivated regions. In addition to the seaboard cultivation, portions of the moorland have been reclaimed by manuring with wrack, and now form isolated addenda to the crofts, as on the peninsula of Ardmhor, or actual crofts as on Bruernish and near the crofting townships on the east coast.

The total area of arable land in Barra amounts to 725 acres, of which 213 acres are under clover and rotation grass, and 512 acres are under tillage. Oats, potatoes, rye and barley (in that order) are the main crops. (Statistics supplied by the Department of Agriculture for Scotland.)

The main feature of the crops on sandy soil is the prevalence of Dicot weeds. A field of barley near Loch St. Clair has the following population of weeds, in descending order of frequency: *Myosotis arvensis*, *Ranunculus acris*, *Chrysanthemum segetum*, *Euphrasia officinalis* agg., *Trifolium repens*, *Stellaria media*, *Cerastium vulgatum*, *Lamium purpureum*, *Vicia cracca*, *Chrysanthemum leucanthemum*, *Bromus hordeaceus*, *Daucus carota*, *Lolium perenne*, *Senecio vulgaris*, *Bellis perennis*, *Artemesia vulgaris* and Oats. Many of these species are present on the adjoining machair. Presumably they have invaded the crop from the machair, or have persisted in the cultivated land ever since it was first farmed. Other fields in similar situations are likewise infested with weeds; some of the hormone herbicides, which are effective against Dicots, might with advantage be used in these situations.

Some of the land round Breveig, to the south and west of the wood, is also cultivated. This region is locally reputed to have been used by one of the Macneils as a vegetable garden, and to have been enriched by boatloads of soil from Ireland. The soil now shows no obvious difference from that in similar situations in other parts of the island. Most of the cultivation here takes the form of hay, which is harvested the first summer, then left as grazing for the next few seasons. A comparison was made between a hayfield and an adjoining meadow which had been grazed for three years. The principal grasses in the hay here are *Lolium perenne*, *Anthoxanthum odoratum*, *Cynosurus cristatus* and *Holcus lanatus*. *Trifolium medium* and *T. dubium* are also (a). Other species present include *Poa pratensis*, *Vicia cracca*, *Ranunculus repens* and *Plantago lanceolata* (f), *Euphrasia officinalis* agg., *Rhinanthus minor* agg., *Juncus conglomeratus* and *Centaurea nigra* (o), and *Aegopodium podagraria*, *Juncus articulatus*, *Senecio jacobaea* (r). Little change has taken place in the three years since the field was laid down to hay. *Holcus lanatus* has become (r), *Trifolium medium* and *T. dubium* (o), and *Ranunculus repens*, *Euphrasia officinalis* agg., *Rhinanthus minor* agg., *Centaurea nigra*, *Aegopodium podagraria*, *Juncus articulatus* and *Senecio jacobaea* have increased in frequency. The less well-drained parts of the field have been invaded by such species as *Iris pseudacorus*, *Caltha radicans*, *Lychnis flos-cuculi* and *Orchis hebridensis*.

Hay is also grown on shallow soil near Scurrival. The subsoil is shingle, and the six inches of soil are peaty in texture but liberally sprinkled with grains of sand blown from the western beaches. Here again there is little difference between the flora of the hayfield and that of the unfenced seaboard grassland. Grasses such as *Poa pratensis*, *Lolium perenne* and *Holcus lanatus* are more frequent in the hay, while a few species such as *Armeria maritima*, *Plantago coronopus* and *Aira pracox* are present in the grassland and absent from the hay.

On the western part of the island, then, the land is rendered suitable for cultivation by the natural deposition of wind-borne sand. This process, though it varies in degree from year to year, is of course a continuous one. On the eastern half of the island, as has been shown, the natural vegetation is heather moor or grass moor, and to render this suitable for cultivation radical changes have to be made in the soil. The normal procedure in Barra, as in the other Western Isles, is the application of wrack or tangle (*Fucus vesiculosus* and *Laminaria* spp.) on top of strips of inverted sods of peat cut from the surface of the moor. The decomposing seaweed raises the pH and provides inorganic salts, while the channels between the lines of manure aid drainage. These *feannagan*, or lazy beds, are first used for potato cultivation, but may later be sown with oats, barley or hay. The changes in soil structure resulting from this application of seaweed persist over a number of years. Table IV gives a comparison of two of these improved areas in Bruernish; one was treated with seaweed two years ago, the other has been untouched for over ten years.

Table IV.

Retrogression to Moorland.

	Recent Cultivation.	Uncultivated for Ten Years.
Festuca ovina	a	a
Plantago lanceolata	f	. .
Sieglingia decumbens	f	o
Cynosurus cristatus	o	o
Holcus lanatus	o	. .
Anthoxanthum odoratum	o	f
Aira flexuosa	o	. .
Agrostis stolonifera	o	r
Prunella vulgaris	o	r
Euphrasia officinalis agg.	o	r
Hieraceum pilosella agg.	o	. .
Plantago maritima	o	f
Potentilla erecta	r	o
Lotus corniculatus	r	. .
Centaurea nigra	r	. .
Calluna vulgaris	local	o–f
Erica cinerea	local	r
Carex echinata	. .	o
Molinia caerulea	. .	f
Scirpus caespitosus	. .	o
Luzula pilosa	. .	o
Carex flacca	. .	o
Succisa pratensis	. .	o
pH	6·0	5·3

As can be seen from the above table, the pH is slowly dropping to that of the adjoining moor, and though the retrogression is slow, perhaps as a result of the steep slope and good drainage, species such as *Calluna vulgaris*, *Molinia caerulea* and *Scirpus caespitosus* are gradually re-establishing themselves. Retrogression of this type is not found in the western half of the island, as the improvement of the soil is undertaken by continuous natural means, viz. the deposition of sand in the soil.

While considering former cultivation and habitation there is one further point of interest. On many of the hilltops of Barra there are remains of Duns, or ancient forts, which have been disused for the last few centuries. Round each of the Duns, however, signs of former habitation are still found in the shape of healthy crops of nettles. These nettles do not spread along the dykes on the adjacent moor.

Pteridium aquilinum is present in Barra, in small quantities, on Bruernish and Ardmhor, round Loch Obe and near Breveig. Nowhere, however, does it show any signs of spreading as it so commonly does on islands such as Eigg and Colonsay. It is known (Fenton, 1936) that cattle help to limit the spread of Bracken, and the number of cattle on Barra (1688) which wander over wide areas may help to explain the relative scarcity of *Pteridium*. Pigs, however, which root up the rhizomes are not generally kept on the island.

E. *Woodland.*

There are three plantations of trees on Barra: one at Breveig, a second near Ardmhor, and a third at Northbay. The ecology of these woods has already been dealt with by Forrest Waterston and Watson (*loc. cit.*). All the trees were planted at the instigation of Lady Gordon Cathcart about sixty years ago. It is suggested by Forrest Waterston and Watson that some of the *Pinus sylvestris* at Ardmhor may be the remains of the forest which originally covered the island. This suggestion, however, is not borne out by the New Statistical Account of Scotland (1845), where it is stated that "*Barray is as defective in the article of timber as any of its neighbouring isles*". There, too, an account is given of an earlier attempt to establish woodland on the island, and the failure of this attempt is attributed to transplantation of the trees to the windswept sandy plains of Eoligarry.

That natural scrub and woodland were formerly present in Barra is shown by the researches of Blackburn (1946), who has analysed a peat from Lochan nam Faoileann. She demonstrated that this region of Barra has always supported a large population of *Ericoid* plants with, in addition, some *Corylus-Betula* scrub, but found at all horizons pollen grains of some forest trees, such as *Pinus Quercus* and *Ulmus*.

F. *Summary.*

The greater part of the island of Barra is covered with peat, which supports vegetation of grass moor, heather moor or mixed moor. Peat for fuel is cut from this moor, and regeneration from the peat cuttings follows a regular sequence from the *Sphagnum*-filled trenches of recently opened cuttings to the *Calluna*-covered surface of the dried trench. Succession on the sand-dunes is of the usual type, but there is considerable development of machair, or sea-meadow, extending for several hundred yards behind the dunes. Blown sand affects the hills on the west coast, causing the formation of grassland instead of moorland. Cultivation is undertaken both on this grassland and on reclaimed areas of moorland. There is at present no natural woodland on the island.

ACKNOWLEDGMENT.

This paper is based on observations made on the Island of Barra in July 1947. The foundation of much of the work, however, was laid in March 1938, when the author was one of a team of Edinburgh botanists who made a preliminary ecological survey of Barra. The work then begun was interrupted by the war and never completed. To my colleagues on that preliminary investigation, Dr. A. S. Boughey, Dr. C. M. Cant and Dr. E. V. Watson, I should like to express my thanks.

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THE VEGETATION OF A SAND-DUNE SYSTEM IN THE OUTER HEBRIDES. By C. H. GIMINGHAM, B.A., A. R. GEMMELL, B.Sc., Ph.D., M.S., and P. GREIG-SMITH, M.A.

(Read 11th March 1948.)

INTRODUCTION.

A detailed examination of a sand-dune system on the west coast of the Isle of Harris was undertaken in July, 1946 and 1947, as a study of dune formation under Atlantic conditions. It was thought that a survey of a maritime plant community in the extreme west might provide useful data for comparison with similar communities in other parts of the country. The area investigated is known as Luskentyre Banks, and occupies a small rounded promontory about half a mile long and quarter of a mile wide on the north side of a relatively large sandy bay (Traigh Luskentyre), which is completely uncovered at low tide. Although facing west, it is protected from the full force of the wind by the island of Taransay, which rises to a height of 875 feet and lies about a mile off the coast. The sand is highly calcareous, consisting largely of finely comminuted shell fragments. The dunes are separated from the blanket bog, which is the dominant vegetation of the island, by a strip of "machair". (The latter term, as Wilmott (1945, p. 39) has pointed out, is used both for fixed dune pasture and for wind-blown sand covering peat.) This is much more fertile than most of the soil on the island, and is the only type on which cultivation can be carried out without the use of "lazy-beds", a system of narrow strips built up with soil from trenches on either side.

Machair areas can be picked out from a distance by the intense green in strong contrast to the general brownish hue of the surrounding vegetation. Most of the machair at Luskentyre is cultivated, but there is a small area of fully fixed dune, lightly grazed but otherwise undisturbed, which will be described.

PHYSIOGRAPHY AND CLIMATE.

The main topographical feature is a series of ridges and valleys running north-east and south-west and rising to 116 feet (Ordnance survey 1″ to 1 mile, 1929 edition). At the west end (see fig. 1) the ground is very broken, forming a small complex of dunes showing the same general trends. The most northerly main ridge is modified by subsidiary valleys running north and south. The whole area is subject to considerable wind erosion. At the western end especially there are numerous steep erosion faces, and the floor of many of the valleys is bare of all vegetation. Locally the sand in these has become cemented to a depth of about one inch on the valley floor, forming a soft calcareous sandstone.

The nearest station for which full meteorological figures are available is Stornoway in Lewis (58° 11′ N., 6° 22′ W.). Rainfall data are also available for Monach, North Uist (57° 31′ N., 7° 42′ W.), and Loch Maddy, North Uist (57° 36′ N., 7° 10′ W.) (Meteorological Office, 1919–24).

TABLE I.

MEAN TEMPERATURE (STORNOWAY), 1919–24.

	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	Year.
Max.	43·7	44·1	45·3	49·5	53·7	58·4	60·2	60·0	57·7	52·2	47·6	44·4	51·4
Min.	34·9	34·2	34·4	37·5	41·3	46·4	48·9	49·0	46·2	41·2	38·0	35·4	40·6
Mean	39·3	39·2	39·9	43·5	47·5	52·4	54·6	54·5	52·0	46·7	42·8	39·9	46·0

TABLE II.

MEAN RAINFALL, 1919–24.

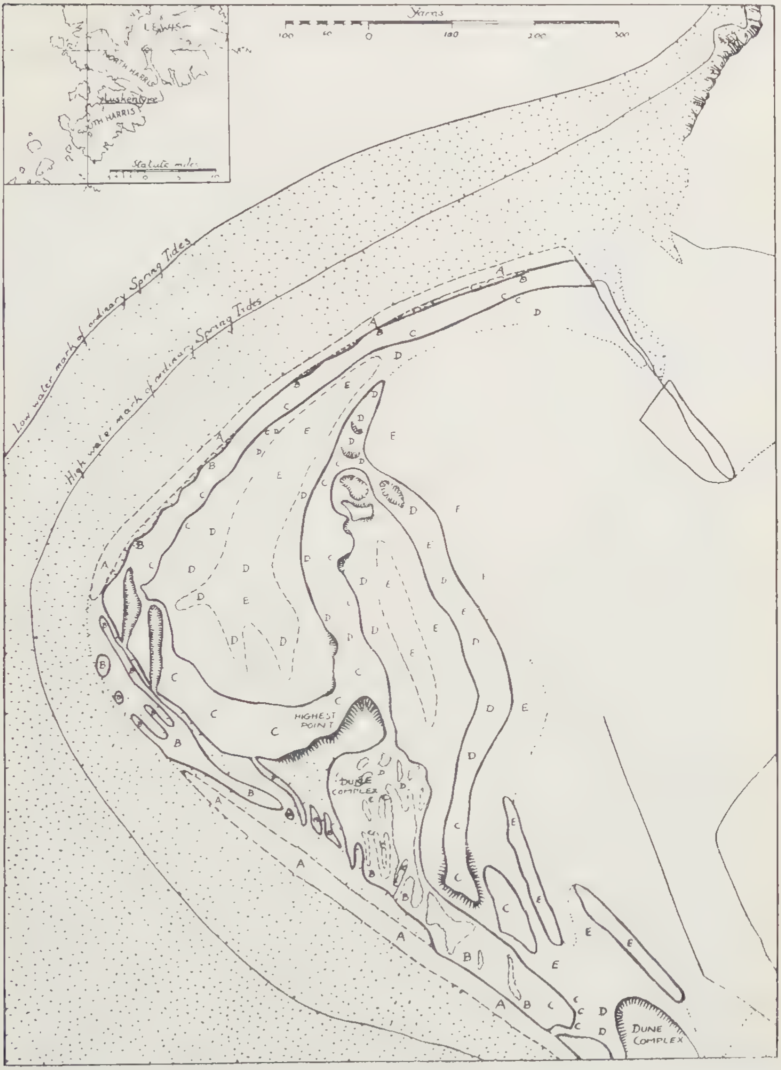
	Stornoway.		Monach.	Loch Maddy.
	In.	Days.	In.	In.
J.	5·17	25	5·01	4·88
F.	4·46	22	4·02	3·97
M.	4·10	24	3·69	3·75
A.	3·03	19	2·77	2·85
M.	2·56	19	2·36	2·63
J.	2·32	17	2·54	2·55
J.	3·03	21	2·90	3·22
A.	3·97	22	3·87	4·12
S.	3·95	21	3·74	4·07
O.	5·18	23	4·48	5·03
N.	5·83	24	5·28	5·23
D.	6·25	26	5·96	5·85
Year	49·85	263	46·62	48·20

From Table I it will be seen that the temperature range is comparatively small, the mean values varying only between 39·2° (Feb.) and 54·6° (July). Summer temperatures are not high, the maxima for July averaging 60·2°, but the winter is relatively warm, with the average minimum in February dropping only to 34·2°. Rainfall (Table II), although not very heavy, is evenly distributed, and the number of rainy days per month is characteristically high throughout the year, reaching an average of 26 in December and falling only to 17 in June.

VEGETATION.

Fig. 1 is a field sketch showing approximately the stage in succession reached in different parts of the dunes in July 1947. "A" represents the foreshore community just above the high-water mark, "B" mobile dunes (corresponding to the white and yellow dunes of various accounts: Tansley, 1939), "C" and "D" are stages in fixation, and "E" is dune pasture. The varying rate of fixation, controlled largely by differences in protection from the full force of the wind, is evident from the mosaic of vegetation types. Full species lists for the five stages are given in Table III. Slacks are absent.

Foreshore Community (*Stage A*).—The practically level, smooth sand above the high-water mark bears a sparse vegetation in which *Ammophila arenaria* is the only species at all frequent. Although occasional plants of *Agropyron junceum* are present, this species does not form a separate zone below the *Ammophila* and appears to play no part in dune formation. The only other associates are *Cakile maritima*, *Arenaria peploides* and *Atriplex ? laciniata*. The usual association of plants with seaweed drift was evident except in the case of *Arenaria*. This point was not examined in detail, but four *Atriplex* and five out of six *Cakile* plants excavated were associated with decaying seaweed drift below the surface. Only for two out of six *Arenaria* plants was this so. No figures are available for *Ammophila* and *Agropyron*, but a considerable proportion of the *Ammophila* seedlings was associated with drift. The difference in behaviour is possibly associated with the deeper root system of *Arenaria*. Four plants of the latter had a mean root depth of 18½ inches (maximum 27 in.); whereas seven *Atriplex* had a mean depth of 6 inches (maximum 8 in.) and ten *Cakile* plants a mean depth of 7 inches (maximum 9 in.). The foreshore is occasionally visited by sheep but only the *Cakile* shows any evidence of grazing.


Yards
100
50
0
100
200
300
NORTH HARRIS
Luskentyre
SOUTH HARRIS
Statute miles
Low water mark of ordinary Spring Tides
High water mark of ordinary Spring Tides
HIGHEST POINT
DUNE COMPLEX
DUNE COMPLEX

Heavy lines enclose ridges.
-.-.-.- lines enclose hollows.
▥ Erosion faces.

A. Foreshore; B. Embryonic Dunes;
C. Early Fixation; D. Later Fixation;
E. Dune Pasture.

FIG. 1.—Map of Luskentyre Banks, Isle of Harris, showing stages in succession reached at various parts of the sand dunes.

TABLE III.

LUSKENTYRE BANKS: SPECIES LISTS FOR FIVE STAGES IN SUCCESSION.

	Stage.				
	A.	B.	C.	D.	E.
× *Ammophila arenaria*	a	a	d	d	f
× *Agopyron junceum*	o	o	r	. .	. .
× *Cakile maritima*	o[1]	o	r[4]	. .	. .
× *Arenaria peploides*	o	r	. .	. .	. .
× *Atriplex ? laciniata*	r	o	. .	. .	. .
Plantago maritima	× ?[2]	. .	. .	. .	. .
Iris pseudacorus	r[3]	. .	. .	. .	. .
× *Cerastium tetrandrum*	. .	o	f–la	o	. .
× *Festuca rubra* var. *arenaria* f. *subglabra*	. .	r	o	f–la	. .
Taraxacum sp.	. .	r	o	o	o
Sinapis arvensis	. .	r	. .	. .	. .
× *Trifolium repens*	. .	. .	f–ld	f	f
Poa pratensis	. .	. .	o–lf[5]	o–lf	a
× *Rumex crispus*	. .	. .	o	. .	. .
× *Holcus lanatus*	. .	. .	o	. .	f
× *Senecio jacobaea*	. .	. .	o	f	f
× *Plantago lanceolata*	. .	. .	o	f	f
× *Cerastium vulgatum*	. .	. .	o	o	o
× *Rumex acetosella*	. .	. .	r	. .	. .
× *Lotus corniculatus*	. .	. .	r	o	o–la
× *Ranunculus repens*	. .	. .	r	. .	. .
× *Bellis perennis*	. .	. .	r	f	f
× *Sonchus asper*	. .	. .	r	. .	. .
× *Galium verum*	. .	. .	. .	a–ld	f–a
Thalictrum montanum	. .	. .	. .	f–la	o
× *Euphrasia officinalis* (agg.)	. .	. .	. .	lf	o
× *Carex arenaria*	. .	. .	. .	o–lf	o
Lolium perenne	. .	. .	. .	lf	f
Festuca rubra var. *glaucescens*	. .	. .	. .	o	a
× *Campanula rotundifolia*	. .	. .	. .	o	o
× *Linum catharticum*	. .	. .	. .	o	o
Ranunculus acris	. .	. .	. .	o	o
× *Polygala vulgaris*	. .	. .	. .	o	o
× *Achillea millefolium*	. .	. .	. .	r	o
× *Leontodon autumnalis*	. .	. .	. .	r	. .
× *Veronica arvensis*	. .	. .	. .	r	. .
Arrhenatherum elatius	. .	. .	. .	r	o–f
× *Prunella vulgaris*	. .	. .	. .	r	o
Poa trivialis	. .	. .	o	r	o
× *Thymus serpyllum* (agg.)	. .	. .	. .	. .	f
Helictotrichon (*Avena*) *pubescens*	. .	. .	. .	. .	o
× *Luzula campestris*	. .	. .	. .	. .	r
Carex flacca	. .	. .	. .	. .	r

TABLE III—*continued.*

	Stage.				
	A.	B.	C.	D.	E.
Rhinanthus stenophyllus	..	..	..	..	r
× *Crepis capillaris*	..	..	..	..	r
× *Geranium molle*	..	..	..	..	r
Primula vulgaris	..	..	..	..	r
Bryum pendulum Schp.	..	..	o	f	..
Mnium undulatum L.	..	..	..	la	r
Camptothecium lutescens B. & S.	..	..	..	f–la	o[6]
Dichodontium pellucidum Schp.	..	..	..	o–la	..
Barbula fallax Hedw.	..	..	..	o	..
Tortula ruraliformis Dixon	..	..	..	o	r[6]
Hylocomium squarrosum B. & S.	..	..	..	o	a
Hypnum cuspidatum L.	..	..	..	r	o
Amblystegium filicinum De Not.	..	..	..	r	..
Cylindrothecium concinnum Schp.	..	..	..	..	a
Hylocomium triquetrum B. & S.	..	..	..	..	la
Brachythecium purum Dixon	..	..	..	..	f
Mnium rostratum Schrad.	..	..	..	..	o
Thuidium delicatulum Milt.	..	..	..	..	o
Lophocolea bidentata Dum.	..	..	..	o	o
Psilocybe ammophila Fr.	..	r	..	..	..
Peltigera sp.	..	..	r	..	o
Nostoc sp.	..	..	..	o	o

---

[1] *Cakile maritima* was much more abundant in Zone A in 1947.

[2] One plant, evidently blown in and re-rooting. Appeared fairly healthy.

[3] A broken piece of rhizome carried in, probably derived from a patch of well-established *Iris pseudacorus* farther up the bay. Was re-rooting actively, but aerial parts, though growing, did not appear very healthy.

[4] ? Relict from Stage B.

[5] Generally with *Trifolium repens.*

[6] Confined to remains of tussocks.

× Species listed by Hepburn (1945) as more or less constant for British sand-dunes.

Mobile Dunes (*Stage B*).—The mobile dunes rise sharply from the shore. Their tops and sides bear a fairly thick, though not closed, cover of *Ammophila*, which appears uniform from a distance but on closer examination shows marked localisation of shoots. The *Ammophila* spreads from the dune sides into the valleys, which are otherwise bare. Only on the tops of the mobile dunes does it flower at all freely. The accompanying species are similar to those of the foreshore and none are frequent. There are occasional plants of *Cerastium tetrandrum* and *Festuca rubra* var. *arenaria* f. *subglabra* which play an important part in later stages.

Fixation (*Stages C and D*).—The vegetation of the mobile dunes grades into Stage C and the latter into Stage D. Stage C is characterised by the local abundance of *Trifolium repens*, *Poa pratensis* and *Cerastium tetrandrum*, which initiate the stabilisation of the bare sand between the shoots of the *Ammophila*. Occasional plants of a few other species characteristic of open habitats are also found. Some of the Stage C vegetation had recently been burnt (probably accidentally) and had a different aspect due to abundant *Senecio jacobaea* and *Bryum pendulum*. The species present on such areas are:

Ammophila arenaria (d), *Senecio jacobaea* (a), *Ranunculus repens* (o), *Cerastium tetrandrum* (o), *Festuca rubra* var. *glaucescens* (o), *Bryum pendulum* (a).

In the later stages tussocking of the *Ammophila* becomes apparent, and in typical Stage D it forms tussocks up to 18 inches in height with very few shoots, living or dead, in the intervening spaces. The localisation of shoots to form the nucleus of these tussocks has been described elsewhere (Greig-Smith *et al.*, 1947). The absence of any eroded shoots between the tussocks suggests that the latter are formed by the accumulation of wind-blown sand around groups of *Ammophila* shoots rather than by erosion in the intervening spaces. On the tops of well-developed tussocks *Festuca rubra* var. *arenaria* f. *subglabra* and *Galium verum* are constantly present, together with occasional plants of *Thalictrum montanum*, *Poa annua*, *Polygala vulgaris*, *Taraxacum* sp. and *Campanula rotundifolia*, while the sides frequently have a cover of bryophytes, especially *Camptothecium lutescens*, *Barbula fallax*, *Tortula ruraliformis* and *Dichodontium pellucidum*. Between the tussocks there is an almost closed vegetation cover formed of a considerable number of species of which *Galium verum*, *Festuca rubra* var. *arenaria* f. *subglabra* and *Thalictrum montanum* are the most prominent (see Table III). Stage D is the earliest in which bryophytes play any important part, and locally an almost closed society is formed, principally by *Barbula fallax* and *Dichodontium pellucidum*.

Dune Pasture (*Stage E*).—With the establishment of a completely closed community, conditions appear to become unfavourable for *Ammophila*. The dune pasture at the back of the ridges next to

TABLE IV.

RECOLONISATION ON ERODED SURFACES.

1. Early stage on the side of an erosion scoop. Open community between *Ammophila* tussocks.
2. As 1. Later stage. Fairly closed community with a high proportion of bryophytes.
3. As 1. Bottom of scoop.

4 and 5. Recolonisation on bared slopes.

	1.	2.	3.	4.	5.
× *Ammophila arenaria*	a	f	f	f	a
Festuca rubra var. *glaucescens*	f	a	a	a	a
× *Thymus serpyllum* agg.	f	a	f	..	..
× *Linum catharticum*	f	o	r	o	o
× *Trifolium repens*	f	a	o	o	r
× *Sedum acre*	f	r	..	lf	f
× *Cerastium vulgatum*	f	o	o	..	f–la
† *Scleropoa (Festuca) rigida*	f	..	..	..	f
× *Bellis perennis*	o	f	a	a	a
× *Polygala vulgaris*	o	o	r	..	..
Poa pratensis	o	f	f	f	f
× *Galium verum*	o	o	a	o–lf	o
× *Senecio jacobaea*	o	f	o	f	f
× *Plantago lanceolata*	r	f	a	f	f
† × *Valerianella olitoria*	..	f	..	..	..
× *Lotus corniculatus*	..	f	..	o	o
× *Holcus lanatus*	..	o	f	r	..
× *Veronica arvensis*	..	o	..	r	..
× *Luzula campestris*	..	o	o	o	o
× *Euphrasia officinalis* agg.	..	o	f	..	f
Helictotrichon (Avena) pubescens	..	o	..	..	..
× *Geranium molle*	..	r	..	..	..
× *Crepis capillaris*	..	r	..	..	..
× *Prunella vulgaris*	..	r	..	..	..
† × *Anthyllis vulneraria*	..	r	..	..	..
× *Ranunculus repens*	..	r	..	r	..
† *Coeloglossum viride*	..	r	..	..	..
Rhinanthus stenophyllus	..	r	..	..	..
† *Daucus carota*	..	r	..	..	..
Poa trivialis	..	..	la	..	..
× *Achillea millefolium*	..	..	f	..	..
† *Odontites rubra*	..	..	f	..	..
† *Viola* sp. (leaves only)	..	..	o	lf	..
× *Campanula rotundifolia*	..	..	r	o	..
× *Cerastium tetrandrum*	..	..	..	a	..

† Species not found in the primary succession.

× Species listed by Hepburn (1945) as more or less constant for British sand-dunes.

Table IV (*continued*).

	1.	2.	3.	4.	5.
Taraxacum sp.	..	..	..	r	..
† *Ranunculus acris*	..	..	..	r	..
Ranunculus sp. (leaves only)	..	..	..	..	r
Camptothecium lutescens B. & S.	a	a–ld	a	f	f
Tortula ruraliformis Dixon	f	..	..	f	a
Dichodontium pellucidum Schp.	r	..	..	a–ld	ld
Hylocomium triquetrum B. & S.	..	a–ld	..	..	..
Thuidium delicatulum Milt.	..	f–la	..	..	..
Brachythecium purum Dixon	..	f	o	..	..
Cylindrothecium concinnum Schp.	..	o	r	..	..
Hylocomium squarrosum B. & S.	..	r	f	..	..
Mnium rostratum Schrad.	..	..	r	..	..
Barbula fallax Hedw.	..	..	..	f	f
† *Mnium hornum* L.	..	..	..	..	o
Mnium undulatum L.	..	..	..	..	o
Lophocolea bidentata Dum.	..	f	o	..	..
Peltigera sp.	..	o	..	o	f
† ? *Leptogium sinuatum* Massal. var. *scotinum* Leight	..	..	..	o	o
Nostoc sp.	f	..	..	f	f

† *Equisetum variegatum* and † *Ditrichum flexicaule* also occur locally in recolonised areas but were not present in any of those listed.

† Species not found in the primary succession.

the cultivated machair shows remains of *Ammophila* tussocks, and stages in their breakdown can be traced. In the fully established dune pasture the vegetation is a rather loose turf of *Festuca rubra* var. *glaucescens* and *Poa pratensis* with abundant *Galium verum*. *Ammophila* is still frequent but occurs as scattered stunted flowerless shoots. The list of accompanying species is similar to that of Stage D, with the addition of a number of typical grassland plants, e.g. *Helictotrichon* (*Avena*) *pubescens* and *Luzula campestris*.

Secondary Succession on Eroded Surfaces.

Table IV gives species lists from several examples of recolonisation. Erosion usually results in the removal of all vegetation except *Ammophila*. Sometimes the latter also is removed, when recolonisation may take place from the neighbouring areas by rhizome spread, but apparently without the formation of large tussocks. Once active erosion has ceased, stabilisation of the sand surface takes place rapidly, mainly by the agency of bryophytes—in contrast to the primary succession, where they play only a minor part. The floristic composition is similar to that of later stages in the primary succession. A number of species are marked in Table IV as not found in the primary succession, but most of them are species characteristic of grassland, and only *Scleropoa* (*Festuca*) *rigida* and *Valerianella olitoria* are likely to be peculiar to the subsere.

SOIL.

Soil samples were taken from the surface and at depths of 6 and 12 inches on three transects passing through all five stages of the dune succession.

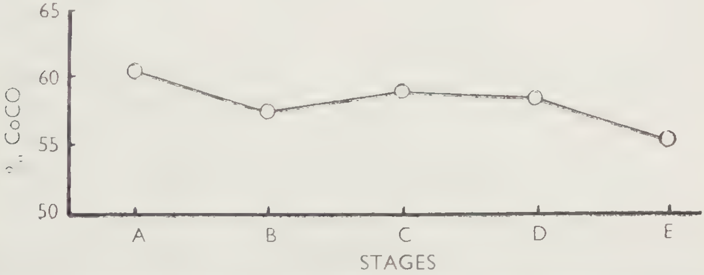


FIG. 2.—Carbonate content at each stage, averaged over transects and depth.

The pH as determined by B.D.H. capillator (Phenol Red Indicator) showed little variation, the range being 7·2–7·6.

The carbonate content was determined by an approximate titration method (see Piper, 1942, p. 136). The result showed the presence of large quantities of carbonate ranging from 48 to 70 per cent. by weight, expressed as calcium carbonate.

When the results were examined statistically a number of points became evident (Table V). Firstly, there was considerable variation between samples, but no significant difference between the carbonate content of the sand samples in any of the five successional stages when summed over depths (fig. 2). Secondly, carbonate content at varying depths summed over stages showed slight but fairly constant variation (fig. 3). Thirdly, a highly significant difference was found between transects, indicating that the major factor influencing the carbonate content of the soil was probably

TABLE V.

PERCENTAGE CALCIUM CARBONATE IN SAMPLES OF SAND.

		Transect.		
		I.	II.	III.
Stage A.	Surface	68	57	56
	6 inches	68	70	61
	12 ,,	60	52	54
Stage B.	Surface	59	50	51
	6 inches	62	56	52
	12 ,,	67	67	55
Stage C.	Surface	54	50	57
	6 inches	60	69	58
	12 ,,	69	64	51
Stage D.	Surface	64 *	62	57
	6 inches	62	53	58
	12 ,,	59	53	61
Stage E.	Surface	52 *	48	48
	6 inches	68	62	65
	12 ,,	61	53	45

* These two samples were lost and the values have been estimated by iterative use of Yates's modified form of Allan and Wishart's formula for missing data (see Snedecor, 1946, p. 268).

ANALYSIS OF VARIANCE.

	Sum of Squares.	n.	Mean Square.	F.	P.
Stages . . .	118·80	4	29·700	1·49	> ·2
Depths . . .	278·53	2	139·267	7·01	·01–·001
Interaction . .	608·13	8	76·017	3·82	·01–·001
Transects . .	370·53	2	185·267	9·32	< ·001
Error . . .	516·80	26	19·877	. .	. .
Total . .	1892·80	42	. .	. .	. .

the rate at which fresh wind-blown sand was deposited in different areas, rather than rainfall which would be uniform over the dune area. Fourthly, there is also a significant zone-depth interaction.

Fig. 3 shows that the mean carbonate content of the surface layer of the soil is 60 per cent. on the foreshore, falling to 53–54 per cent. in Stages B and C and rising again to 61 per cent. at Stage D (the region where *Ammophila* tussocks reach their maximum development and over which deposition of fresh sand might therefore occur more easily). The subsequent drop to 49 per cent. in the dune pasture is the result of leaching in a stage in which accumulation of wind-blown sand is no longer an important factor.

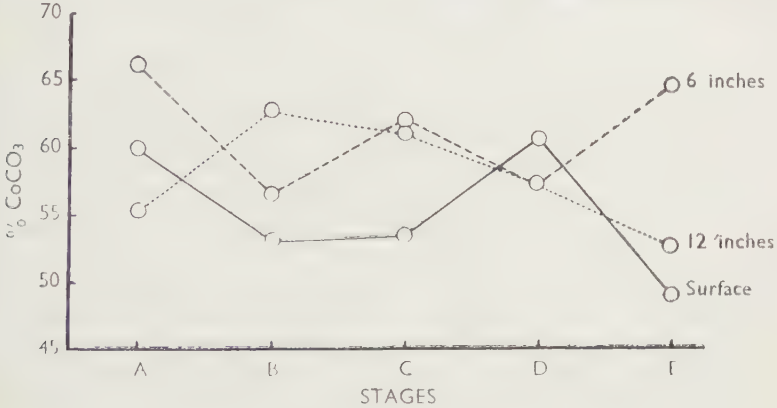


Fig. 3.—Carbonate content at various depths at each stage, averaged over transects.

The data for the samples at 6 inches reflect almost exactly the position in the surface layer, the main difference being that leaching from the surface causes this layer to have a constantly higher carbonate content, except in Stage D where the rate of renewal by freshly deposited sand probably exceeds the rate of leaching.

In Stage A the data for the samples at 12 inches show a loss of 5 per cent. or more, assuming that freshly deposited sand has a content of not less than 60 per cent. This loss is difficult to explain, but may have occurred when the 12-inch layer was originally at the surface, if a temporary cessation of sand deposition had allowed a certain amount of leaching to take place. It might, alternatively, be due to removal by frequent tidal saturation of these deeper layers. In later stages the percentage of calcium carbonate at a depth of 12 inches appears to depend upon the amount retained at 6 inches. Thus in Stage B the content at 12 inches is considerably higher than at 6 inches, whereas at Stages C and D they are approximately equal. The conditions established in Stage E are such that the carbonate leached from the surface accumulates mainly at the 6-inch level.

The above results differ in certain respects from those obtained by Salisbury (1922, 1925) at Blakeney and Southport. The carbonate content of the dunes in these localities (averaged over depths of 0–8 or 9 inches) decreases with the progress of succession; and the rate of leaching is high at first, decreasing as the carbonate content becomes lower. The Luskentyre dunes, however, have a very much higher initial content, exceeding even the value determined by Salisbury for dunes at Bundoran in Donegal (11·4 per cent.). Further, the dune systems at Blakeney and Southport are more regular and stable than those at Luskentyre, and sand accretion ceases to be important after the "yellow dune" stage. During the frequent high winds at Luskentyre, however, sand deposition appears to be appreciable in all areas except those now covered by dune pasture (Stage E), which are partially sheltered behind the main ridges. The degree of leaching of carbonate in the successive stages and its differential accumulation at varying depths present a much more complex picture at Luskentyre than at Blakeney and Southport.

Discussion.

Accounts of dune vegetation on the west coast of Scotland are few. Forrest *et al.* (1936) give a brief account of dunes in Barra. They describe four zones corresponding broadly in floristic composition to the Stages A, B, C–D and E described here (no frequencies are given). Wilmott (1945) gives notes on species of flowering plants from dunes in Uig, Lewis. Watson (1939) gives a list of the principal mosses from dunes in Barra.

The succession on the Luskentyre dunes appears to follow a course similar to that described on most British dunes, with *Ammophila* as the principal dune builder, but the succession is much checked and interrupted by the violent winds to which the area is exposed. The subordinate rôle of *Agropyron junceum* is noteworthy. In some dune systems it is absent, but where present it normally forms a separate zone of foredunes to the seaward of the *Ammophila* dunes. Hepburn (1945) has analysed fifteen accounts of dune vegetation, including both acidic and calcareous types, and has drawn up a list of species more or less constantly found on dunes. Species in this list are marked " × " in Tables III and IV. It will be seen that Hepburn's list includes most of the species of flowering plants from Luskentyre, the exceptions being mainly of weed or grassland type probably derived from the neighbouring crofts.

The most noteworthy feature of the Luskentyre dune vegetation is the very subordinate part played by cryptogams. In contrast to those of the calcareous dunes of the west coast of England (Watson, 1918 *a*), the bryophytes at Luskentyre are comparatively few and in the primary succession play only a minor part in the stabilisation of the surface. In the secondary succession they appear to have a rôle more like that in the English dunes, being the main stabilising agents.

Not only are the bryophytes of minor importance in the vegetation, but some of the species present are unexpected. *Dichodontium pellucidum* is commonly regarded as at least preferentially calcifuge (*e.g.* by Amann (1928), who lists it among Swiss species found only on neutral substrata, pH 7·0), while Watson (1918 *b*) considers it pronouncedly calcifuge. *Mnium* spp., *Hypnum cuspidatum* and *Ambylstegium filicinum* are species normally found only in moister habitats, frequently occurring in dune slacks. Their presence on the dunes may perhaps be correlated with the uniformly rainy climate of the Outer Hebrides.

SUMMARY.

An account is given of the vegetation of a sand-dune system on the west coast of the Isle of Harris, Outer Hebrides.

In the initiation of the dunes the main part is played by *Ammophila arenaria*, *Agropyron junceum* having only a minor rôle. Bryophytes play little part in the primary succession but on eroded surfaces they are the main sand stabilisers.

The sand in all parts of the dunes is highly calcareous. An account is given of the carbonate content at the surface and depths of 6 and 12 inches at various stages in the succession.

The vegetation is compared with that of other British dune systems.

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SPORE DEVELOPMENT IN ARCHEGONIATE PLANTS.

By ELIZABETH M. KNOX, M.A., B.Sc. (With Pl. III.)

(Read 17th June 1948.)

During the last twenty years attention has been focused on microspores found in coals and their value for purposes of correlation of coal seams. Few of the many recorded fossil spores can be related with certainty to their parent plants, and their classification is necessarily an arbitrary one, based upon differences in the appearance of the exospores. It is, therefore, desirable to know something of the mode of formation of the spore walls, and at what stage in development the sculpturing is initiated; and whether the microspores show any marked variation in ornamentation of their walls during maturation, and whether differences in form can be recognised as growth takes place. The value of the spore analysis of coals depends to a large extent upon an exact definition of spore types, and it is essential to have a clear understanding of the possible range of variation in sculpturing within the species which may be due to immaturity or other causes. It was in the hope of finding a solution to some of these problems that the present study of the development of spores in the Archegoniatae was undertaken as part of a more comprehensive work on the microspores of fossil and modern plants.

Observations have been based mainly on an examination of sporogenesis in *Lycopodium* and *Selaginella*, but opportunity has been taken to include references to the work of other investigators and to review briefly the somewhat extensive literature on the subject.

In modern *Lycopodiales* spore development follows a definite course, and a similar pattern can be traced, with slight modification, throughout the Bryophyta. Briefly, the general plan is, that by repeated division of the archesporial cells a mass of sporogenous tissue is formed, delimited by one or more layers which form the sporangial wall. All the sporogenous cells are potential spore mother cells, though in certain cases some of them may disintegrate, and, together with the tapetum, serve a nutritive function for the developing spores.

In the genus *Lycopodium* the sporangia begin to develop when the sporophyll is still composed of embryonic cells. The curved row of archesporial cells, by repeated divisions, gives rise to sporogenous tissue (Pl. III, fig. 1), nearly all of which functions as spore mother cells. These become rounded, separate from one another, and included in a viscous fluid or plasmodium (Pl. III, fig. 2), where they undergo the tetrad division (Pl. III, fig. 3). External to the sporogenous mass are three or more layers of cells, of which the innermost differentiates to form a nutritive tissue or tapetum. In *Lycopodium*, unlike most other Pteridophytes, there is little or no disintegration of the tapetum during spore development.

The development of the microsporangia in *Selaginella* is essentially similar to that described for *Lycopodium* (Pl. III, figs. 6–15), though in the former, the tapetum is derived from the outermost layer of sporogenous cells (Bower, 1935). In *Selaginella* all the cells of the sporogenous tissue are potential spore mother cells, but 10–20 per cent. may disintegrate according to Lyon (1901). The functional spore mother cells round off and separate from one another during the reduction division (Pl. III, figs. 7, 11). Each of the four microspores formed by tetrad division is broadly pyramidal with a rounded base (Pl. III, figs. 9, 14).

In both genera, when the nucleus of the spore mother cell divides, nuclear plates form across the spindles (Pl. III, fig. 3) and the mother cell divides into four tetrahedrally arranged spores. In those spores which finally bear reticulate, spinose or other form of ornamentation, the pattern appears on the outer rounded sides of the spores very soon after the tetrad division has occurred and while the spores are still within the mother cell membrane (Pl. III, figs. 3, 7, 12). The spores enlarge to fill the cavity of the spore mother cell and their sculpturing becomes rapidly more pronounced. The spore mother cell wall then disintegrates and the tetrads are set free (Pl. III, figs. 9, 14). The sculpturing on the exospore is initiated almost immediately and, according to Lyon (1901), spines are laid down by deposition of material derived from the liquid between the exospore and the mother cell membrane. The tetrads continue to enlarge after they are set free, until the spores attain the mature form and size and finally separate (Pl. III, figs. 5, 10, 15).

The details of sporangial development in *Equisetum* differ slightly from those pertaining to the *Lycopodiaceae*. The sporogenous tissue is surrounded by irregular layers forming the sporangial wall, with the innermost layer functioning as a tapetum. During the course of spore development there is a disintegration of the tapetum and of all except the outer layers of the sporangial wall. Cells of the sporogenous tissue round themselves off as spore mother cells; only two-thirds of these cells undergo the tetrad division, the remainder become disorganised, their substance mingling with that of the tapetum and becoming apparent as a multinucleate plasma in the interstices between the spore mother cells (Smith, 1938). This fluid persists until the spores are almost mature. The spores of *Equisetum* are all alike and have a wall composed of four layers (Beer, 1909); the outermost is laid down in four spiral strips, which later split from the remainder of the wall, except for one common point of attachment; these form the elaters and originate, according to Beer, from the tapetal cytoplasm. The exospore and endospore are the products of the spore protoplast. The superficial cells of the sporangium wall become indurated and spirally thickened.

A similar condition to that found in *Equisetum*, where only some of the cells of the sporogenous group are fertile, is characteristic of *Tmesipteris*, *Psilotum*, *Ophioglossum* and *Helminthostachys* (Bower, 1894). In these genera the remainder of the potential spore mother cells become disorganised and scattered throughout the mass; their substance being absorbed by the developing fertile spores. In some ferns the spores, after the tetrad division, may become detached from one another while still enclosed within the spore mother cell membrane (Steven, 1905). The spore mother cell membrane subsequently disappears and the individual spores lie embedded in the tapetal plasmodium, where they enlarge and build a sculptured wall about themselves.

In the Bryophyta generally a proportion of the sporogenous tissue remains sterile, and either forms elaters as in the *Jungermanniales*, or degenerates and functions as a nutritive fluid (Campbell, 1905).

Among the *Ricciaceae* all the sporogenous tissue within the sporogonium forms potential spore mother cells, though a few may degenerate. The spore mother cells round off and a disintegration of their walls begins to take place. This breaking down of the spore mother cell membrane, as well as of some of the cells of the wall of the sporophyte, results in a viscous fluid in which the actively dividing spore mother cells are suspended; the chief function of this immersing fluid is that of providing a food supply for the developing spores. After the tetrad division the four spores remain within a common sheath until the spore walls are nearly mature. The fully developed spore wall is composed of three layers and is irregularly thickened and folded (Smith, 1938; Black, 1913; Beer, 1906).

Sporogenesis in *Reboulia* follows a similar course. The spore coats are laid down in centripetal succession by the activity of the plasma membranes (Blair, 1926).

Again in the *Sphaerocarpales* the spore wall is generally composed of three layers (Siler, 1934). In the winged spores of *Riella*, the wing is formed from the layer within the spore mother cell wall and is part of the perineum (Wigglesworth, 1937). Folds and thickenings appear in this layer and from its outer surface spines arise, which are a characteristic feature of the spores of Riella (Howe and Underwood, 1903). This development takes place within the spore mother cell wall, which on maturation of the spores is found to disappear.

It can thus be claimed that fundamentally the same pattern of development is seen to run through the whole of the Archegoniatae, and it is of interest to note that where comparable fossil material has been studied similar developmental stages have been observed. For example, in sections of Lepidostrobus, it is found that the outer wall of the sporangium is thickened and the spores contained within it are frequently united in tetrads, and in this condition exhibit small spines on their surface and have also developed the equatorial flange so characteristic of spores of *Lepidodendron*.

Calamostachys is a cone with recognised affinity to *Equisetum*. It has a sporangial wall with the spiral thickenings so characteristic of Equisetales, as well as the smooth walled spores, frequently seen united as tetrads within the spore mother cell wall and embedded in a non-cellular matrix (Hirmer, 1927). The spores of the tetrad may vary in size, one being large and three small or *vice versa*, or some spores may abort; this condition in the fossil cones has been cited by Scott (1920) as a possible indication of the origin of the heterosporous condition.

A more advanced type of sporogenesis is described by Radforth (1938, 1939) in the fossil *Senftenbergia*, a genus related to the *Schizaceae*. The fossil genus follows closely the Fern type of development.

The Bryophyta have also their fossil counterparts, as described by Harris (1938), for the spores of *Naiadites*. These spore bear a striking resemblance to the winged forms of *Riella*, with which they have probable affinity.

There is thus no reason to doubt that spore formation, development and maturation have followed the same pattern amongst the Archegoniatae throughout geologic times. Certain facts may therefore be deduced with regard to fossil spores in respect to the formation of the spore walls and their ornamentation. It is evident from the instances given above that the sculpturing on the exospore is usually initiated while the tetrad of spores is still contained within the spore mother cell wall; and in all cases the final form of ornamentation is foreshadowed at an early stage, and there is no suggestion of differences of form during development or of a graded series such as has been postulated for certain fossil spores (Moore, 1946). Only spores in which the wall has become cutinised are capable of preservation as fossils, and such spores already exhibit the type of sculpturing characteristic of the adult. The assumption is thus justifiable that microspores found in coals, if they have not actually reached maturity, will at least have the characteristics of the adult and can be classified as belonging to the same type.

ACKNOWLEDGMENTS.

I am indebted to Professor Sir William Wright Smith for material and facilities to carry out this investigation; to Professor John Walton I am grateful for allowing me the opportunity to examine slides of the Kidston Collection; and to the Carnegie Trustees I am indebted for a grant in aid of research.

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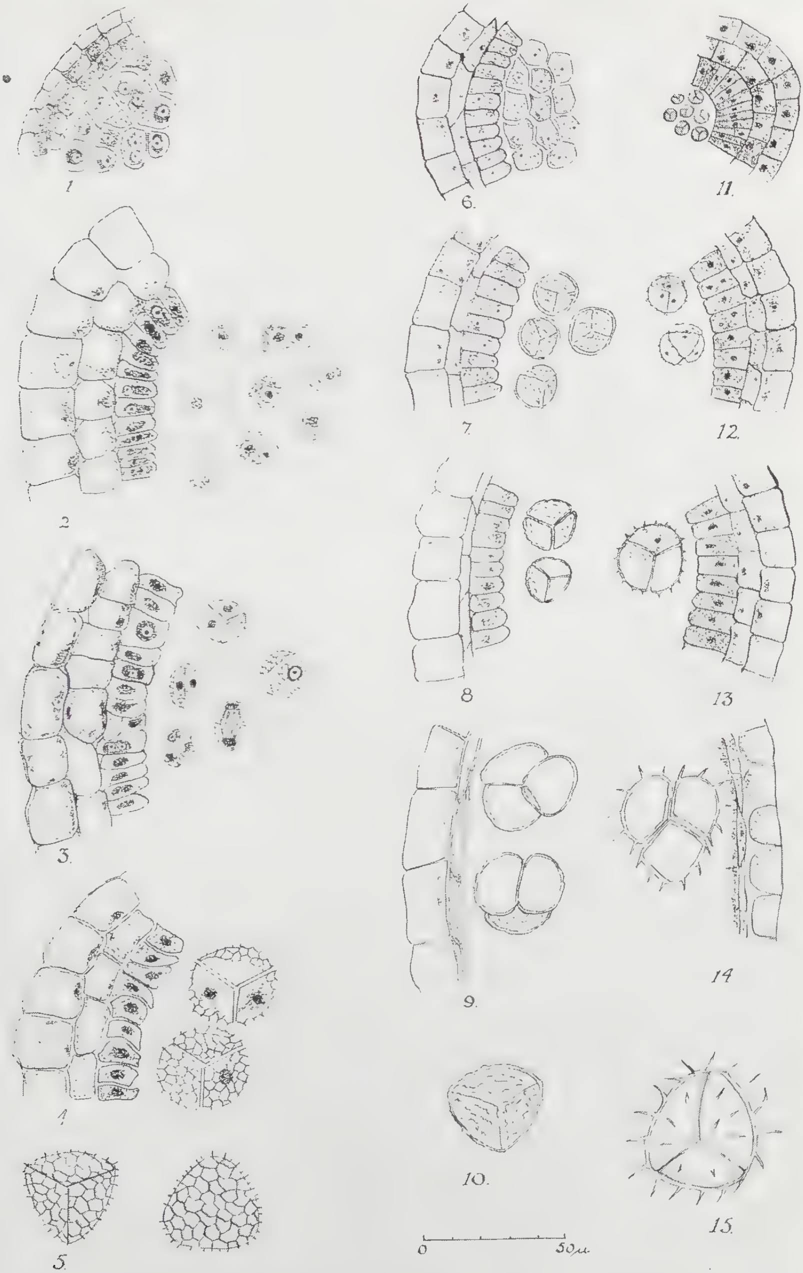
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Figs. 1–5.—Development of sporangia and spores in *Lycopodium alpinum*.
Figs. 6–10.—Development of sporangia and spores in *Selaginella Martensii*.
Figs. 11–15.—Development of sporangia and spores in *Selaginella selaginoides*.
All × 375.

REPORT OF THE ANNUAL CONFERENCE OF THE CRYPTOGAMIC SECTION, 1947.

By C. E. FOISTER, B.A., Ph.D.

(Read 20th May 1948.)

The Cryptogamic Section of the Society held the Fifty-ninth Annual Conference in the Dunkeld district on 26th–28th September 1947, with headquarters at the Royal Hotel, Dunkeld.

A foray was held on 26th September along Butterstone Loch and in the adjoining woods, a very good collection of microfungi, especially rusts, being made in perfect weather conditions. The Perthshire Natural History Society were represented in this and other forays. At the evening business meeting, among other matters, it was agreed to hold the next annual conference in the Thornhill district and that the Dumfriesshire and Galloway Natural History and Antiquarian Society should be invited to join in the forays. It was also agreed to submit suggestions to the Council for a Cryptogamic Conversazione at one of the meetings.

On 27th September forays were held along the Tay at Inver, where a good agaric collection was made in the damp woods lining the river, and in the Murthly Castle grounds, a good collection representative of most groups resulting. In the latter grounds, the famous yew avenue and the uncompleted Murthly Castle were seen, while a visit was also paid to Dunkeld House grounds to see the trees which provided the seed for the famous Dunkeld Hybrid Larch. On 28th September a visit was paid to the Ballinluig and Pitlochry districts, the weather being exceptionally fine, but apart from a few exceptional fungi the collection was not very good.

The Society was indebted to Sir Edward Mountain, Mr. Fotheringham and the Atholl Estates, Ltd., for permission to visit their grounds, while it should be recorded that assistance in identifications was given by Dr. M. Wilson and Dr. J. Grainger. Dr. Wilson has kindly assisted in checking the list given below of the fungi and other groups collected. The forays were considered very successful, the beautiful scenery of this district adding to the pleasure of the nineteen members who attended.

Dr. J. A. Macdonald has drawn attention to the fact that the record in the Trans. Bot. Soc. Edin., 34: 4, 394, of the host of *Uromyces genistae-tinctoriae* should read *Cytisus scoparius.*

LIST OF CRYPTOGAMS COLLECTED.

FUNGI.

HYMENOMYCETES.

Amanita mappa (Batsch) Fr. ; nitida Fr. ; phalloides (Vaill.) Fr. ; rubescens (Pers.) Fr.
Anellaria separata (L.) Karst.
Armillaria mellea (Vahl) Fr.
Bolbitius titubans (Bull.) Fr.
Boletus badius Fr. ; chrysenteron (Bull.) Fr. ; edulis (Bull.) Fr. ; flavus (With.) Rea ; luridus (Schaeff.) Fr.
Calocera cornea (Batsch) Fr.
Cantharellus aurantiacus (Wulf.) Fr. (=Clitocybe aurantiaca (Wulf.) Studer.).
Collybia butyracea (Bull.) Fr. ; radicata (Rehl.) Berk. ; velutipes (Curt.) Fr.
Coprinus micaceus (Bull.) Fr. ; radiatus (Bolt.) Fr.
Entoloma jubatum Fr.
Exobasidium vaccinii (Fck.) Woron. on Vaccinium myrtilis L.
Fomes annosus Fr. ; fomentarius (L.) Fr.
Ganoderma applanatum (Pers.) Pat. ; lucidum (Leyss.) Karst.
Hydnum repandum (L.) Fr.
Hygrophorus pratensis (Pers.) Fr. ; virgineus (Wulf.) Fr.
Hypholoma fasciculare (Huds.) Fr. ; velutinum (Pers.) Fr.
Inocybe rimosa (Bull.) Fr.
Irpex obliquus (Schrad.) Fr.
Laccaria laccata (Scop.) B. & Br. ; also var. amethystina (Vaill.) B. & Br.
Lactarius piperatus (Scop.) Fr. ; rufus (Scop.) Fr. ; subdulcis (Pers.) Fr. ; subumbonatus Lindgr. ; velutinus Bertillon.
Lepiota cristata (A. & S.) Fr.
Marasmius hariolorum (DC.) Quél.
Nyctalis asterophora Fr. on Russula nigricans (Bull.) Fr.
Mycena alcalina Fr. ; galericulata (Scop.) Fr. var. calopus Fr. ; haematopus (Pers.) Fr. ; hiemalis (Osbeck) Fr. ; pura (Pers.) Fr.
Panus conchatus (Bull.) Fr. ; stipticus (Bull.) Fr.
Phylacteria terrestris (Ehrh.) Big. & Guill. on Fraxinus excelsior L.
Pistillaria quisquiliaris Fr. on Pteridium aquilinum (L.) Kuhn.
Pleurotus ostreatus (Jacq.) Fr.
Pluteus cervinus (Schaeff.) Fr.
Polyporus betulinus Fr. ; intybaceus Fr. ; schweinitzii Fr. on Larix europaea DC. ; sulphureus (Bull.) Fr.
Poria vaporaria (Pers.) Fr.
Psalliota arvensis (Schaeff.) Fr.
Radulum orbiculare Fr. on wood of Betula alba L.
Russula atropurpurea (Krombh.) Maire ; emetica (Schaeff.) Fr. ; nigricans (Bull.) Fr. ; ochroleuca (Pers.) Fr.
Stereum hirsutum (Willd.) Fr. on Alnus glutinosa (L.) Gaertn. ; spadiceum Fr. on Alnus glutinosa (L.) Gaertn.

GASTEROMYCETES.

Lycoperdon depressum Bon. ; perlatum Pers.
Phallus impudicus (L.) Pers.
Scleroderma aurantium Pers.

UREDINALES.

Coleosporium senecionis Fr. on Senecio vulgaris L. ; tussilaginis Kleb. on Senecio jacobea L. and Tussilago farfara L.

Cronartium ribicola Fisch, de Waldh. on Ribes nigrum L.

Gymnosporangium juniperi Link on Sorbus aucuparia L.

Melampsora hypericorum Wint. on Hypericum androsaemum L. and H. pulchrum L. ; saliciscaprearum Kleb. on Salix atrocinerea Brot.

Melampsoridium alni Diet. (=M. hiratsukeanum Sto.) on Alnus glutinosa (L.) Gaertn. ; betulinum Kleb. on Betula pendula Roth.

Milesia blechni P. Magn. on Blechnum spicant (L.) Roth. ; kriegeriana (Magn.) Arth. on Dryopteris spinulos var. dilatata (Hoff.) Undrw. ; polypodii B. White on Polypodium vulgare L.

Phragmidium mucronatum (Pers.) Schlecht. on Rosa canina L. agg. ; violaceum (Schultz) Wint. on Rubus fruticosus L. ; rubi-idaei (DC.) Karst. on Rubus idaeus L.

Puccinia Andersoni Bel. Br. on Carduus heterophyllus L. ; agropyrina Erikss. on Agropyron repens (L.) Beauv. ; airae Cruch. & Mayor on Deschampsia caespitosa (L.) Beauv. : annularis Schecht. on Teucrium scorodonia L. ; anthoxanthi Fck. on Anthoxanthum odoratum L. ; arrhenatheri Erikss. on Arrhenatherum elatius (L.) J. & C. Presl. ; caricis Reb. on Carex sp.; centaureae DC. on Centaurea nigra L. ; chaerophylli Purt. on Anthriscus silvestris (L.) Hoffm. ; cirsii-lanceolati Schroet. on Cirsium vulgare (Savi) Ten. ; graminis Pers. on Avena sativa L., Agropyron repens (L.) Beauv., Agrostis tenuis Sibth. ; holcina Erikss. on Holcus mollis L. ; lapsanae Fck. on Lapsana communis L. ; luzula-maximae Diet. on Luzula sylvatica (Huds.) Gaud. ; malvacearum Mont. on Malva sylvestris L. ; menthae Pers. on Mentha spp. ; mirabilissima Peck on Mahonia aquifolium (Pursh) Nutt. ; phragmitis Körn. on Phragmites communis Trin. ; pruni-spinosae Pers. on Prunus domestica L. ; pulverulenta Grev. on Epilobium sp. ; punctata Link on Galium cruciata (L.) Scop. ; violae DC. on Viola riviniana Rchb.

Pucciniastrum epilobii Otth. on Chamaenerion angustifolium (L.) Scop.

Thecopsora vacciniorum Karst. on Vaccinium myrtillus L.

Uromyces fabae de Bary on Vicia sp. ; geranii Otth. & Wart. on Geranium sylvaticum L. ; valerianae Fck. on Valeriana officinalis L.

USTILAGINALES.

Entyloma ranunculi (Bon.) Schroet. on Ranunculus repens L.

Tilletia holci (Westend.) Schroet. on Holcus mollis L.

Tubercinia trientalis B. & Br. on Trientalis europaea L.

Ustilago violacea (Pers.) Rous. on Silene cucubalus Wibel.

ASCOMYCETES.

Aleuria aurantia (Oed.) Phil.

Chlorosplenium aeruginosum (Oed.) de Not. on Alnus glutinosa (L.) Gaertn.

Claviceps purpurea (Fr.) Tul. on Anthoxanthum odoratum L., Arrhenatherum elatius (L.) J. & C. Presl., Dactylus glomeratus L. ; Deschampsia caespitosa (L.) Beauv. and var. mollis, Festuca sp., Holcus lanatus L.

Coryne sarcoides (Jacq.) Tul.

Dasyscypha calycina (Schum.) Fck. on Larix decidua Mill.

Elsinoe veneta (Burkh.) Jenkins on Rubus fruticosus L.

Erysiphe cichoracearum DC. on Heracleum sphondylium L.; polygoni DC. on Heracleum sphondylium L.
Helotium citrinum (Hedw.) Phil.
Keithia thujina Durand on Thuja plicata D.Don.
Leotia lubrica (Scop.) Fr.
Leptosphaeria acuta Moug. on Urtica dioica L.
Leptothyrium alneum (Lév.) Sacc. on Alnus glutinosa (L.) Gaertn.
Lophodermium rhododendri Ces. on Rhododendron sp.
Microsphaera quercina (Schw.) Burr. on Quercus robur L.
Mycosphaerella fragariae (Tul.) Lindau on Fragaria virginiana cult.
Nectria cinnabarina (Fr.) Fr. on Sarothamnus scoparius (L.) Koch; galligena Bres. on Pyrus communis L.
Phacidium ilicis Lib. on Ilex aquifolium L. ribis on Ribes nigrum L.
Pseudopeziza trifolii (Fr.) Fck. on Trifolium pratense L. & T. repens L.
Rhopographus pteridis (Sow.) Rab. on Pteridium aquilinum (L.) Kuhn.
Rhytisma acerinum Fr. on Acer pseudo-platanus L.
Sclerotinia curreyana (Berk.) Karst. on Juncus effusus L.
Sphaerotheca humuli (DC.) Burr. on Filipendula ulmaria (L.) Maxim.; pannosa (Wallr.) Lév. on Rosa canina L. agg.
Taphrina potentillae (Johan.) Tub. on Potentilla erecta (L.) Räusch; tosquinetii (Westend.) Magn. and alni (B. & Br.) on Alnus glutinosa (L.) Gaertn.
Uncinula aceris (DC.) Sacc. on Acer pseudo-platanas L.
Xylaria carpophila (Pers. ex Fr.) Fr. on Beech mast; hypoxylon (L. ex Fr.) Grev.

PHYCOMYCETES.

Peronospora parasitica (Fr.) Tul. on Acer pseudo-platanus L., Capsella bursa-pastoris (L.) Medic., Digitalis purpurea L. and Senecio jacobea L.
Phytophthora infestans (Mont.) de Bary on Solanum tuberosum cult.

IMPERFECTI.

Cladosporium fulvum Cooke on Lycopersicum esculentum Mill.
Cristulariella depraedens (Cke.) v. Höhnel on Acer pseudo-platanus L.
Hapalosphaeria deformans Syd. on Rubus fruticosus L.
Ovularia obliqua (Cke.) Oudem. on Rumex obtusifolius L.
Polythrincium trifolii Fr. on Trifolium repens L.
Ramularia primulae Thüm. on Primula vulgaris Huds.; violae Trail on Viola riviniana Rchb.
Septoria aegopodii (Preuss) Sacc. on Aegopodium podograria L.
Sporocybe azaleae (Peck.) Sacc. (=Pycnostysanus azaleae (Peck) Mason) on fruits of Rhododendron sp.

LICHENS.

Evernia furfuracea Mann.
Peltigera canina Willd.

MOSSES.

Catharinea undulata W. & M.
Dicranum scoparium Hedw.
Fontinalis antipyretica Ren.
Hylocomium splendens B. & S.

Mnium undulatum L.
Plagiothecium undulatum B. & S.
Polytrichum commune L. ; juniperinum Willd.
Thuidium tamariscinum B. & S.

FERNS.

Asplenium adiantum-nigrum L. ; ruta-muraria L. ; trichomanes L.
Athyrium filix-femina (L.) Roth.
Blechnum spicant (L.) Roth.
Cystopteris fragilis (L.) Bernh.
Dryopteris fragilis (Bak.) C.Chr. ; filix-mas (L.) Schott ; spinulosa (Müll) Warr.
Osmunda regalis L.
Phyllitis scolopendruim (L.) Newm.
Polypodium phegopteris L. ; vulgare L.
Thelypteris oreopteris (Ehrh.) C.Chr. ; palustris Schott. ; phegopteris (L.) Slosson.

TRANSACTIONS

OF THE

BOTANICAL SOCIETY OF EDINBURGH

SESSION CXIII

Presidential Address: Microspores and their Significance in Biological Problems. By Elizabeth M. Knox, M.A., D.Sc.

(Read 20th January 1949.)

During the last thirty years the study of pollen grains, and spores in general, has come to be recognised as a significant branch of biological science. The value of this study—palynology, as it is now called—is becoming apparent in an increasing number of quite unrelated investigations, and is proving particularly useful in the elucidation of some of the problems of palaeobotany and palaeoecology. For the present purpose the term microspore will be used in a comprehensive sense to cover the great variety of small spores found in spore-producing plants, including the Angiosperms, in which the microspore is represented by the pollen grain.

On account of their size, ranging from 15 μ to 250 μ, the morphological study of microspores has necessarily been associated, to a large extent, with the development of the compound microscope. One of the first microscopes, described by Hooke in his "Micrographia" in 1665, though to our eyes a crude instrument, had nevertheless many important and far-reaching effects on the scientific work of the seventeenth century. Two of Hooke's contemporary microscopists, Grew in England and Malpighi in Italy, gave a good account of the structure of pollen grains, and recognised their structural variation in different groups of plants, which at that time was no small achievement. Thereafter little work of any importance on pollen morphology was done for over a century, until Francis Bauer, described as "botanical painter to George III and resident draughtsman to the Royal Botanic Garden, Kew," made sketches of pollen grains to accompany his drawings of plants, but, unfortunately, his drawings were never published. Before the time of Bauer's death, in 1840, a sudden increased interest in spore morphology became evident, no doubt connected with considerable improvements in the microscope: among investigators of the period who made notable contributions were Purkinje, von Mohl, Mirbel, and Fritsche. Of these naturalists, Purkinje became famous principally as a physiologist, and his name is commemorated in the Purkinjian nerve cells of the cerebellum, and the Purkinjian fibres of the cardial muscle. It is of interest to recall also that to him are due the introduction to botany of the terms protoplasm and cambium, and that he was the discoverer of Canada Balsam as a mounting medium. Amongst his many contributions to science his researches on pollen grains led to his recognition of the phylogenetic importance of pollen grain morphology, a great advance on the views of his predecessors.

Towards the end of the eighteenth century and beginning of the nineteenth, investigations on pollen centred mainly on the problem of fertilisation. Many theories were advanced, and although the growth of a pollen tube was known, the pollen grain was regarded as a vesicle containing "fertilising" granules capable of independent movement; these were supposed to travel down the pollen tube and to be discharged among the cells of the ovary. The movement of the granules was investigated by Robert Brown in 1828, and from his experiments on both organic and inorganic substances he came to the conclusion that the vibration of the particles was a property of nearly all matter, inherent in the particles themselves, and not due to extraneous causes. It is from Robert Brown's researches on pollen grains that the phenomenon known as Brownian movement gets its name. Von Mohl's treatise on pollen morphology, published in 1834, stands out as a work of major importance. He was the first botanist to advance a descriptive classification of pollen grain structure, based on the number of spore coats and the number of germinal furrows, and the first to recognise their significance. Following von Mohl, Fritsche formulated a classification of pollen grains based primarily upon the absence or presence of furrows and their number, and it is to this author that the terms exine and intine for the spore membranes are due. Since he was a chemist rather than a botanist, he did a considerable amount of chemical analysis of the contents of pollen grains and of their membranes. It remained, however, for Hugo Fischer, in 1890, to expand the knowledge gained and to bring the science of pollen morphology to something approaching its modern position. After his time few fundamental advances were made for almost a century, until Wodehouse published his admirable monograph on "Pollen Grains" in 1935, which is now the standard work on the subject.

In this book Wodehouse discusses the characteristic features of spore morphology which are of most significance; he also demonstrates those which are of special importance from the point of view of classification and phylogeny. The spores of mosses and ferns or seed plants are invariably formed in the same way, as a result of a tetrad division within a spore mother-cell. Considering the uniform mode of formation it would be natural to expect spores to be constructed along similar lines from the simplest mosses to the most advanced flowering plants; and this, broadly speaking, is the case. From the point of view of the spore morphologist, the construction of the wall and its associated features are of prime importance. The spore wall usually exhibits two or more layers. The outermost layer or perine, when present, is arranged more or less loosely outside the part of the wall called the exine and follows the outline of the exine fairly closely. In the special case of Equisetum the elaters are formed from the splitting up of the perine. The exine constitutes the main part of the spore wall, and may itself be of two layers, an outer thicker one, usually provided with sculpturing of some kind, and an inner thin layer. Between the exine and the protoplasm within the spore is a thin intine from which the pollen tubes are formed, and these emerge through pores or furrows in the exine. In the description and classification of spores, their size, shape, characters of the wall and arrangement of the apertures are regularly used; the same features are of importance to the systematist and taxonomist.

As with other organisms, both hereditary and environmental factors go to the shaping of the spores. Since they are formed in tetrads, and usually set free as individuals, their environmental influences are of two kinds, those of the pre-natal or internal environment and those of the post-natal or external environment. The internal environment due to the interaction of the four members of the tetrad upon one another is the main factor in influencing the arrangement of the germinal furrows and the number of germ pores, as well as the type of symmetry in pattern and sculpturing. The external environment tends mainly to modify the sculpturing, while hereditary characters are manifest in the degree of similarity shown between related species.

The pollen grain of the Spermaphyta may be regarded as the equivalent of the microspore of the Pteridophyta. In all the microspores of the Pteridophyta the point of attachment of a spore to other members of the tetrad is seen as a tri-radiate mark or a longitudinal slit, the form of slit being the direct result of the plane of division of the spore mother-cell. Since pollen grains are formed in a similar manner, corresponding sutures might be expected on them also, at least in the more primitive families. To a modified extent this is true; for example, we find in fossil Gymnosperms some pollen grains have a tri-radiate mark such as *Cycadocephalus Sewardii*, and others a longitudinal slit as in *Williamsonia Lignieri* and *Wielandia augustifolia.* Among living Gymnosperms the pollen grains of Cycadales are broadly ellipsoidal with a single deep longitudinal furrow. This is unquestionably a primitive form of grain and foreshadows the many varied and elaborate types met with in more highly evolved Gymnosperms and Angiosperms. The one-furrowed grain which is prevalent throughout the Cycadales is characteristic of many Monocotyledons and primitive Dicotyledons; for example, Palmaceae, Magnoliaceae and Nymphyaceae. Its stability and persistence in these divergent groups are in keeping with the antiquity of their character. The one-furrowed spore appears to have been the starting-point from which the many elaborate and varied forms of grain in both Gymnosperms and Angiosperms have evolved.

"The living Cycads," as Wodehouse points out, "are the last remnants of a venerable and once prosperous race. They are represented by nine genera, widely scattered and extremely isolated in distribution. This is what would be expected of the vanishing remnants of a race of formerly world-wide distribution. In other words, they are going the way of the Cordaitales, Bennetitales and the Ginkgoales, plants whose pollen grains were burdened with a single exaggerated furrow with no adequate measure of closure. May it not be more than a coincidence that these plants perish while Gymnosperms and higher Angiosperms which devised means of protecting or eliminating the primitive furrow gained the ascendancy?"

The study of spore morphology has been instrumental in elucidating diverse problems which arise in quite unrelated sciences. Spores are to be found in many different places: in the air, the soil, or the depths of the ocean, and from their ubiquity are used as indices for a wide range of purposes. Thus the archaeologist is enabled to give a date to buried objects, and the biological history of moors and prairies can be traced, and likewise the history of forest vegetation, or the early history of agriculture as reflected in the pollen-grain remains of weeds and cultivated grasses. From a study of lake sediments and glacial deposits, the rate of deposition can be estimated. The recent work of Professor Hans Peterson of Gothenburg in analysing cores of deep-sea bores has indicated the possibility of revealing the history of submarine beds. Again, from the investigation of pollen in honey it is possible to determine the country of origin; or from pollen in ancient honey from Egyptian tombs, or the dry remains of mead in old drinking horns, interesting information becomes available. To the criminologist, also, spores found in mud on shoes or clothing may yield valuable clues, or to the pharmacologist pollen grains sometimes are important in the qualitative analysis of dry powders.

From the medicinal point of view there has grown up within recent years, both in Europe and America, an extensive literature on pollen in relation to Hay Fever. The principal factor causing Hay Fever is apparently the wind-pollinated plants, which produce vast quantities of pollen. In early spring such flowering trees as elm, oak, poplar, birch and willow scatter large amounts of pollen; while the early summer incidence of Hay Fever coincides with the flowering of the common grasses. The exact species of pollen affecting the sufferer can be ascertained by a specialist by means of a skin test. For this purpose the doctor provides himself with extracts of pollen from different species of plants likely to cause Hay Fever, and which grow in the vicinity of the patient. In making his collection of material the doctor has as his guide the results of a botanical survey of the region or, better still, an aerobiological survey. To make such a survey of the air content, many ingenious devices are used; for instance, the air is sucked in through filters on which the spores are trapped, or plates are exposed, and smeared with suitable substances, to catch the pollen grains. The latter method has been used to investigate the vertical distribution of spores in the air by holding them on plates exposed in aeroplanes at different altitudes. Such researches have revealed that the attack of rust on Canadian crops may be due to wind-blown spores from the south, rust spores having been found at altitudes as high as 5000 metres.

For the theory of pollen statistics it is important to obtain some idea of the total amount of pollen which settles per square unit in periods of varying duration, *e.g.* one summer, one year, or a series of years. With this object in view, investigations have been carried on in several parts of Europe and America under different conditions and at various altitudes. Plates smeared with a thin layer of petrolatum or a coating of glycerine jelly are exposed to the air for a given period of time, *e.g.* twenty-four hours, and results tabulated.

In order to gain an objective idea of the composition of the pollen settling on a bog, it is necessary to investigate the pollen sedimentation of a large number of sample areas, the surface receptivity of the bogs, and the process of transformation of recent material into fossil substance, and of the ultimate result of these processes. With such detailed problems the theory of Pollen Statistics is concerned; and this is now recognised to be an important part of the science of Pollen Analysis.

The presence of pollen in peat was known about 1880 and studied carefully by the Swiss geologist Früh, who realised its importance in relation to the origin and composition of peat deposits. Towards the last decade of the nineteenth century, Weber and Lagerheim began to study the relative proportions of different kinds of pollen in peat. These researches culminated in the launching of the new science of Pollen Analysis by the Swedish geologist von Post in 1916. He refined the methods used and indicated how pollen analysis might be applied so as to give information on problems related to the geology and palaeontology of the Quaternary Period.

Since 1919 Dr. Erdtmann has pursued extensive pollen analytical investigations in Europe, particularly in countries bordering the North Sea, as well as in America. He has been largely responsible for introducing British and American scientists to pollen studies as a method of geological investigation and correlation.

The application of the technique of pollen analysis to post-glacial sediments has proved a useful tool for tracing the sequence of vegetational change. From information thus gained, climatic sequences have been inferred and both vegetational and climatic changes have been correlated with geomorphological change. Thus pollen analysis of interglacial deposits both in Europe and America has revealed the general course of vegetation and climate between the glacial periods.

The use of Pollen Analysis as a palaeo-ecological research method depends upon certain assumptions and rests upon a few facts simple in themselves but complex in their interpretation. The salient fact upon which the whole science is based is that the form of the pollen grain is specific, though different species of a genus may be indistinguishable from one another. Since the most dominant trees have anemophilous pollen, there will be an average mixture of pollen grains of all the available species over a given region; and further, many pollen grains fall on a bog surface, settle and are then preserved under antiseptic and low-oxidation conditions. The peat or sediment accumulates annually and in this way stratified pollen deposits occur. With proper sampling and counting the correlation of stratigraphy–time–vegetation–climate can result. There are certain sources of error which have to be guarded against in the interpretation of the records; *e.g.* the differential preservation and the extent of dissemination by wind, the convergence of some pollen types and the different quantities of pollen produced by trees of various genera may result in distortion of quantitative relations of the fossil spectra. Despite these several weaknesses, pollen statistics give a general picture of the forest cover over a wide area and not merely a local representation of the vegetation of the bog itself.

The deductions from the pollen record relating to climate are not so satisfactory and are still inconclusive. Many factors other than climate affect the composition of vegetation, as for instance topographic changes due to erosion or deposition, or changes in biotic succession leading to climax vegetation formation. Until the relation between the modern distribution of trees and climate is better understood, the interpretation of the past must remain uncertain.

The earliest fossil records of indubitable pollen are from sediments of Jurassic age. Though spores with a tri-radiate mark have been found in sediments of Cambrian age, they become abundant only during the Carboniferous. The reason for the perfect preservation of pollen and spores during these millions of years is that the exines are very resistant to all morphological change during fossilisation. Though the chemistry of the spore exines is imperfectly known, they are found to resist the action of most solvents, including fuming nitric acid, a fact which makes the extraction from sediments possible. Methods essentially similar to those used in pollen analysis have been applied with considerable success to the extraction of spores from coals of different ages. Important differences, however, have to be taken into account in the study of coal. The most striking difference between pollen analysis of peat and spore analysis of coal is that, whereas with pollen in recent deposits most of the species found can be related to modern genera of plants, with the spores from older formations no natural relationship can be determined with certainty. It is therefore necessary to consider carefully the fossils associated with the spores in order to learn something of their palaeo-ecological significance. A further difference is due to the fact that coal has undergone a much greater degree of compression and alteration than peat and therefore methods of sampling, extraction and examination have to be modified, and the criteria used in correlation have to be varied.

Though the science of spore analysis of coal is as yet in its infancy, certain claims can be made for it. During the last twenty-five years the practical importance of the study of spores in coal has been realised, and the possibility of using both megaspores and microspores as an aid to correlation has been demonstrated. They can also be used as indicators of the continental conditions at the time of preservation, and further study may lead to a knowledge of plant migration in Palaeozoic times.

Megaspores were used in the first instance, and studied in thin sections of coal. The technique for examination and recording of megaspores was developed by Theissen in America, and following him in this country considerable work has been done by Slater and Eddy. The method of examination and determination by means of thin sections has definite limitations in that the megaspores as seen in section are cut at different angles and it may be difficult to ascertain the true shape and to recognise variations in spore types. Nevertheless, the method used in conjunction with microspores has been found of value and has recently proved a success in elucidating stratigraphical problems in the Yorkshire coalfield.

In Poland and the Silesian coalfields, Zerndt perfected a method of isolating megaspores from the coaly matrix and used them for the correlation of seams. He was able to distinguish fifty or more types, which are drawn and described in his valuable monograph on the subject. The large size of the megaspores—up to 5 mm. in diameter—and the fragile nature of some of the appendages, render them more difficult of extraction and a less reliable index of plant life than the smaller and more robust microspores, which occur in coals in vast numbers and great variety, and in which the sculpturing on the exine is very perfectly preserved in most cases. These factors have rendered the microspores a useful aid in problems of stratigraphical sequence in coalfield geology.

The microspores are separated from the coal by chemical treatment, which removes the humified material, leaving only the resistant spore-cases for microscopic examination.

The classification of microspores derived from coal in this country has been an entirely arbitrary and artificial one, based upon the thickness and ornamentation of the wall. The spores were arranged in seven groups, designated A, B, C, etc., and the several varieties within each group assigned a number, thus A1, A2, and so on. For practical purposes and for use in correlation of coal seams this has proved quite adequate, but with the increasing use of microspores for purposes of correlation it has become evident that to relate types found in this country with those described in America and by continental workers it is now essential that a binomial nomenclature should be adopted. At the present time such a classification is under review based upon the extensive work of the American palaeobotanists, Schopf, Wilson and Bentall, and when completed should be of value in elucidating some of the wider problems of palaebotanical plant distribution and migration.

The output of spores during Carboniferous times, from arborescent *Lycopods, Calamites, Pteridosperms* and other plants, must have been prodigious. Together with other plant remains the spores collected in vast quantities in swamps which produced coal. The spores preserved, in different coal seams of a succession, occur in varying frequency, and this feature, which can be expressed in the form of spore-frequency diagrams, shows the percentage of types for each seam. The method, or some modification of it, is employed by geologists as an aid in solving problems of short-range correlation. It has been found that for a single seam traced laterally the graph usually remains of similar form over the coalfield; whereas the graph for a seam higher or lower in the succession will have a different general form, resulting from varying proportions between the constituent spore types. For long-range correlation this method is not so reliable owing to a tendency to repetition of the form of diagram at different horizons; thus, for correlation over an extended range a few easily recognised types with a known and definite range are used after the same manner as zone fossils in palaeontology. By means of these characteristic types it is possible to indicate fairly accurately to which subdivision of the Carboniferous system any seam may belong. It has also been possible to suggest a connection between the occurrence of certain spore types and floral zones, which in turn can be linked up with the zoning of the Carboniferous strata by means of non-marine lamellibranchs, thus giving an indication of general biotic conditions at the time of deposition.

The immense number and variety of spores found in coals is an indication of the richness of the vegetation of Palaeozoic times. It has been possible to assign very few of the fossil spores to their parent plants, but with further data and increased knowledge of fossil floras more exact identification may become possible. In assigning fossil spore types to groups of plants a broad view of the fossil record has to be taken as well as of the existing Cryptogamic groups.

The luxuriance of the Carboniferous floras is well known and the whole period is marked by a definite floral sequence and evolution of plant types. A gradual shift in the dominance of various plant groups occurs during the period. In the Lower Carboniferous, coenopterid ferns and lepidodendrids are the chief components of the vegetation; while later the Cordaitales begin to diversify and become conspicuous, and the Pteridosperms gain ascendancy. The Upper Carboniferous is marked by a great development of ferns and pteridosperms and extinction of older forms of Lepidodendron, Sigillaria, Calamites and Neuropterids. In this country spore analysis of coals has been confined almost entirely to the Productive Coal Measures, and it has been possible tentatively to suggest that certain types are of Calamite and others of Lepidodendroid origin, though in general no definite allocation of spores to a family can justifiably be maintained. Many of the spore types are probably of pteridospermic affinity, but the majority might be expected to be of Pteridophytic and Bryophytic origin. It is therefore of interest to consider some of the modern spores of these phylla, and a comparative study suggests a close resemblance between them and certain Carboniferous microfossils.

Among living Pteridophytes the tetrahedral type of spore is most common, but in the primitive family Psilotaceae the spores are bilateral, an interesting contrast to the tetrahedral spores of the early Devonian fossils *Rhynia* and *Hornea*. *Equisetum* possesses spherical, thin-walled, finely granular spores—a type which occurs commonly in coals of Carboniferous age. In the genus *Lycopodium*, spores having surface pits on the walls are characteristic of species belonging to the subgenus *Urostachya*. The subgenus *Rhapalostachya* is characterised by the reticulate type of spore architecture. Great variety in ornamentation occurs in *Selaginella* where the microspores are smooth, granular, spinose, tuberculate, or warty, while some species exhibit a characteristic winglike extension of the spore wall. These features have all been recognised among the fossil forms in coals.

Among the familes of Filicales, the spores show great variation in size and form; those of the Schizeaceae are characteristic and distinctive. The unusual features of the spores of *Aneimia*, together with the Schizeaceous type of sporangia, helped to confirm the placing of the fossil *Dactylotheca plumosa* in this family by Radforth.

Among living Bryophyta, particularly the Hepaticeae, there are some spores with form and sculpturing which bear striking resemblance to some of the Carboniferous microspores. There is also more than a possibility that fungal spores are represented in the fossil record.

Before we can have any certainty of the relationship between fossil spores and their living prototypes, much work will require to be done on both living and fossil microspores.

I have tried to indicate some of the problems which centre round these tiny spores and pollen grains, which are important not only scientifically but also from the economic point of view. For future palynologists there still remain interesting disclosures to be made, whether the material be from Arctic bogs or tropic seas, from Swiss mountain air, Australian honey, glacial clays, Tertiary or Carboniferous coals, or simply from the stamens of plants the systematic position of which is still obscure.

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THE GERMINATION OF GOODYERA REPENS (L.) R. BR. IN FUNGAL EXTRACT. By D. G. DOWNIE, Ph.D.

(Read 17th June 1948.)

In a previous publication (Downie, 1940) it has been shown that on a substrate of glass wool, and with water as a medium, the seed of *Goodyera repens* will germinate provided that its fungal symbiont is present. No external source of carbohydrate or accessory growth substance is necessary, and in three months embryos penetrated by the fungus will increase from 0·2 mm. in length to green-tipped protocorms three or four times the size. Initial activation of growth may be observed when pelotons of hyphae are present in the basal cells and before digestion of the filaments has taken place (Mollison, 1943). From this it may be deduced that substances secreted by the coiled hyphae supply the initial stimulation. Such substances are probably secreted by external hyphae into the surrounding medium, yet non-penetrated embryos, even though surrounded by hyphae, do not germinate. As these secretory substances have passed through the hyphal wall it is unlikely that their molecular construction inhibits passage through the embryo cell walls and we are led to the conclusion that the concentration of the stimulatory substance is fundamental. The metabolic activity of the hyphae within the living cell is likely to be much higher than that of hyphae in water and, in contrast, therefore, to the conditions in the external medium, a much greater secretion of stimulatory substances is released into the smaller volume of the cell sap. Experiments with concentrations of hyphal secretory substances have been made, but these, so far, have proved ineffective in embryo stimulation.

Beyond this initial activation, further growth is coincident with an increased number of embryo cell infections and with the digestion of the hyphae within many of the host cells. On digestion many products of hyphal metabolism are made available to the host. The nearest approach to assessing the effect of at least some of these substances is by using, as a medium, extracts of crushed hyphal filaments. Such an extract was prepared from the symbiont of *Goodyera repens* and proved effective in germination.

Burgeff (1934, 1936) obtained germination and development of seedlings of Phalaenopsis and Eunanthe by adding extracts of the symbiotic fungus to his basal medium, the resultant growth being proportional to the amount of extract added. He isolated from his extract a thermostable substance soluble in water and in absolute alcohol, capable of being absorbed by animal charcoal but not by filter-paper, and regarded it as a vitamin near the "Bios" of Wildiers. Scheffstein (1938) showed that Phalaenopsis seedlings are stimulated by addition to the basal medium of extracts of various plant tissues as well as by extracts of *Rhizoctonia mucoroides* and various yeasts. He demonstrated also that the seed of Phalaenopsis contains very little vitamin. Later, many investigators tested the effect of known vitamins on orchid embryo development. Withner (1942) working with Cattleya hybrids found that the addition of any one of the following vitamins to his basal medium produced no better plants: thiamin, riboflavin, pyridoxine, pantothenic acid, inositol, nicotinic acid, and ascorbic acid. Noggle and Wynd (1943), working with a Cattleya hybrid, found that on a medium containing a purified maltose the addition of thiamin, ascorbic acid and calcium pantothenate had no effect on germination. Germination and growth varying in degree were obtained, however, on the addition of riboflavin, pyridoxine and nicotinic acid.

The majority of investigators interested in orchid seed germination confine their experiments to tropical orchids or their hybrids, and use as a basic medium agar solutions of nutrient salts plus sugar. On such a medium, containing as it does soluble carbohydrates and traces of vitamin, a large number of orchid seeds undergo initial activation although further growth is not maintained. The European terrestrial orchid *Goodyera repens* germinates freely on a medium containing sugar, and therefore to detect initial stimulation a sugar-free substrate devoid of growth substances must be used. Thus, in the experiments carried out in this investigation, whether with known vitamins or with fungal extracts, the basal medium is either water or water with nutrient salts in solution, and the substrate on which the seeds are sown consists of strips of glass wool. Under such experimental conditions the seeds of *Goodyera repens* have given negative germination results with the following known vitamins: thiamin, calcium pantothenate, riboflavin, nicotinic acid, amino-benzoic acid, biotin, inositol, pyridoxine hydrochloride and folic acid, either used singly or together. A hot-water extract of the endophytic fungus, on the other hand, effected germination and growth of the embryos.

FUNGUS EXTRACT OF RHIZOCTONIA GOODYERA REPENTIS.

An isolate of the endophytic fungus of *Goodyera repens* was cultured on a liquid medium consisting of nutrient salts (Pfeffer's solution) and 2 per cent. dextrose (Kerfoots pure bacteriological). After ten days' growth the fungus mats were removed and washed in running water for six hours to remove all traces of dextrose from the mycelium. The mats were dried on filter-paper, transferred to a solution of nutrient salts, and disintegrated in a Waring blender. Part of the resultant mixture was filtered through a Buchner and a Seitz bacterial filter and transferred to sterile test-tubes containing strips of washed glass wool (cold extract). Prior to similar filtrations the other part of the mixture was subjected to a temperature of 70° C. for one hour (hot extract). Preliminary investigations showed that better results were obtained with the hot extract, so that further examination was confined to this solution.

FRACTIONATION OF HOT EXTRACT.

Dr. Forsyth of the Macaulay Institute for Soil Research fractionated part of the hot extract by adding three volumes of absolute alcohol, thus separating alcohol soluble and insoluble substances. The precipitate was centrifuged off and the alcohol-insoluble portion was taken up in distilled water. This solution was filtered through a Seitz bacterial filter and tubed (alcohol-insoluble fraction). The supernatant liquor was evaporated to dryness *in vacuo* and taken up in distilled water. Part of this was reserved for sugar tests, the other part Seitz-filtered and tubed (alcohol-soluble fraction).

REDUCING SUGARS IN FUNGUS EXTRACT.

As the seeds of *Goodyera repens* germinate in concentrations of glucose as low as 0·1 per cent., it was essential to know whether the fungus extract contained sugar and, if so, in what concentration. Dr. Forsyth therefore concentrated part of the alcohol-soluble fraction of the extract for reducing sugars by the method of paper chromatography. Minute amounts of glucose, fructose and ribose were detected. Of these sugars, ribose is the most interesting as it is the sugar component of nucleic acid. Withner (1942) demonstrated that the addition of ribose (2 mg./litre) to a basic nutrient medium containing 2 per cent. dextrose produced, in asymbiotic culture, seedlings which were darker green in colour and had better root systems than the control.

Dr. Forsyth further estimated the exact amount of each sugar present by the method of Flood, Hirst and Jones (1947), weighing in xylose as a standard. In 100 ml. of the fungus extract he found 1·78 mg. glucose, 1·35 mg. ribose, and 0·84 mg. of fructose.

GERMINATION EXPERIMENTS.

Seeds of *Goodyera repens* were sterilised in calcium hypochlorite solution, washed in sterile water, and sown on the glass-wool strips in the experimental solutions. These solutions consisted of (1) hot extract of fungus; (2) alcohol-soluble fraction of this extract; (3) alcohol-insoluble fraction; (4) basic nutrient solution (Pfeffer plus trace elements) plus the three sugars, glucose, ribose and fructose, in the concentrations determined as present in the extract; (5) basic nutrient solution (Pfeffer plus trace elements). For each experimental medium six test-tubes were set up. The cultures were kept for five months in an incubator at 60° F. At the close of that period 250 embryos were measured from each experimental medium. Mr. Quenouille of the Statistics Department, University of Aberdeen, examined these results and submitted the following table:

TABLE OF GERMINATION EXPERIMENTS.

Treatment.	Medium.	Average Length of Embryos.	Average Breadth of Embryos.
1	Fungus extract (hot) . .	100·24 ± 2·59	62·01 ± 1·50
2	Alcohol-soluble fraction of extract	83·55 ± 1·57	46·19 ± 0·80
3	Alcohol-insoluble fraction of extract	114·93 ± 3·77	56·22 ± 1·42
4	Basic solution + 3 sugars .	66·95 ± 0·59	36·64 ± 0·40
5	Basic solution . . .	67·25 ± 0·56	36·52 ± 0·33

These figures are based on direct readings of the embryo with a micrometer eyepiece scale. To express them in terms of microns all measurements would have to be multiplied by 3·3.

Treatments 4 and 5 represent control media. From previous experience it was known that treatment 5, consisting of Pfeffer's nutrient salts plus trace elements, would not stimulate growth, but the effect of the addition of glucose, ribose and fructose in concentrations similar to that of the fungus extract (treatment 4) was unknown. It will be seen that no difference exists between treatments 4 and 5. The concentration of sugar present in 4 is evidently insufficient to stimulate growth.

Considerable growth was effected by the fungus extract (treatment 1), and as the sugars are not responsible for this stimulation some other water-soluble substance or substances must activate growth. This substance must be stable at 70° C. though it is known to be inactivated by steam sterilisation and by autoclaving at 120° C.

Growth occurs in both the alcohol-soluble (2) and alcohol-insoluble fractions (3). This suggests that more than one substance, effective in germination, is present in the extract. Although the growth stimulus seems to be greater in the alcohol-insoluble fraction, the long narrow embryos suggest abnormal growth. The substance controlling a more normal development of the embryo may have been removed in the alcohol solution.

While it is interesting to note that a water extract of the endophytic fungus stimulates the development of many embryos, the resultant growth is far inferior to that of embryos penetrated by the fungus.

In conclusion I wish to thank Dr. W. G. C. Forsyth of the Macaulay Institute for Soil Research, and Mr. W. H. Quenouille of the University of Aberdeen, for their kind assistance.

Summary.

1. A water-soluble extract, made from the disintegrated hyphae of the endophytic fungus, stimulated the development of the embryos of *Goodyera repens*.

2. The activating substance (or substances) is stable at 70° C. but unstable at 100° C.

3. This extract contains glucose, fructose, and ribose, but the total sugar concentration present is insufficient to activate growth.

4. Alcohol-soluble and alcohol-insoluble fractions of the extract stimulate development. The growth of the embryos in the alcohol-insoluble fraction was the greater but tended to be abnormal.

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THE GERMINATION OF LISTERA OVATA (L.) R. BR.

By D. G. DOWNIE, Ph.D.

(Read 17th June 1948.)

The material of *Listera ovata* used in the following experiments was obtained from the grounds of the Priory, near Cupar, Fife. Plants with the inflorescence axis still undeveloped were collected at the end of May 1948 and the roots examined for endotrophic mycorrhiza. Many roots were free throughout their length of any endotrophic fungus, but in all plants examined a few roots were affected at least in part. In affected areas two mycorrhizal fungi were found differing markedly in the diameter measurement of the filament. Both fungi were isolated repeatedly and grown in pure culture. In structure they both conform to the form genus *Rhizoctonia*.

ISOLATION METHODS

Two methods were utilised in isolating the endophytes. In the first and more general method the roots, well washed, were immersed for two minutes in dilute mercuric chloride (1 : 1000). After surface sterilisation and re-washing in sterile water to remove the mercuric chloride, small sections were plated on potato dextrose agar. When the hyphae grew out of the host tissue into the medium, small parts from the margin of the colony were transferred to fresh media. A second method was also used wherein single coils or pelotons were isolated and transferred. This method entailed the surface sterilisation of the roots with mercuric chloride and careful washing with sterile water. The roots were then cut into small fragments and a few fragments placed in a test-tube with sterile water. The fragments were disintegrated with a sterile glass rod and the coils were seen to rise free in the water. Drops of water containing these coil suspensions were introduced into plates of clear agar and incubated at 25° C. for 24–48 hours. Pelotons, which renewed growth on the agar, were then ringed with a single-spore cutter and transferred to potato dextrose agar. If, as is believed, pelotons develop from the invasion of a single hypha, the fungus mat derived from one coil inoculation is comparable to a single spore culture. The isolates used in the germination experiments were obtained by this second method.

SPECIES OF RHIZOCTONIA ASSOCIATED WITH LISTERA OVATA.

Comparative studies of the two species of *Rhizoctonia* isolated from *Listera ovata* have not yet been made with named members of the genus. The larger form is fast growing on potato dextrose agar. The filaments measure 5 μ in diameter, and the oidia average 28×12 μ. The smaller species grows slowly on potato dextrose agar. The diameter of the vegetative hypha is 1·4 μ, and the oidia average 7×5 μ.

SEEDS OF LISTERA OVATA.

Seeds of *Listera ovata* were collected on 16th August and sown three days later. The seeds are small and cream-coloured, with the embryos averaging in size 125×93 μ. The viability of the seed stored in dry conditions in the laboratory is limited to a few weeks, but if sown in water shortly after they are shed from the capsules, the embryos remain viable for many months and increase slightly in size. The seeds were sterilised in calcium hypochlorite and washed repeatedly in sterile water before sowing on the experimental media.

GERMINATION EXPERIMENTS.

As the present experiments were in the nature of a preliminary investigation into the germinating capacity of this orchid, all culture media were used in the form of agar slopes. More critical studies, using glass wool as a substrate, will follow this report. Tests were run on water-agar, with and without nutrient salts (Pfeffer plus trace elements), and on nutrient salt solutions plus dextrose, with and without 50 per cent. potato extract. Each test comprised six test-tubes, the uninoculated tubes not only serving as controls to the fungus-inoculated tubes but also demonstrating the germination capacity of the seeds of *Listera ovata* in asymbiotic culture. The cultures were incubated at 60° F. for six months and at the close of that period 100 random seeds from each experimental medium were measured. The results are tabulated below.

MEASUREMENT OF EMBRYOS AFTER SIX MONTHS.

Medium.	Without Fungus.	Small Fungus.	Large Fungus.
Distilled water agar	138 × 108 μ	412 × 243 μ	155 × 124 μ
Pfeffer agar	130 × 102 μ	350 × 183 μ	142 × 111 μ
Pfeffer agar + 1 per cent. dextrose agar	128 × 100 μ	Embryos parasitised	Seeds completely embedded in fungus mat.
Pfeffer agar + 1 per cent. dextrose agar + 50 per cent. potato extract	130 × 102 μ	834 × 463 μ	. .
Size of embryo at seed dispersal	125 × 93 μ	. .	. .

ASYMBIOTIC GERMINATION.

No asymbiotic germination was recorded on the experimental media. The seed remains viable for at least six months on a moist substratum such as agar medium. Increase in the size of a few embryos was noted particularly in the distilled-water series. This enlargement is not due to further growth but to a marked increase in cell size in the non-meristematic region. In no instance was the swelling great enough to rupture the seed-coat. In the absence of the symbiotic fungus, therefore, no germination of the seed of *Listera ovata* takes place in water or nutrient salt solution. Further, the addition of dextrose or dextrose and potato extract to the basal medium does not activate the growth of the embryos.

SYMBIOTIC GERMINATION.

A. *Small Endophytic Fungus.*—The slender species of *Rhizoctonia* grew sparsely on the distilled water and basic salt media. Most of the embryos penetrated by the fungus were stimulated to grow and in six months many had increased to five times their original size. A few infected embryos were completely parasitised. Non-infected embryos remained dormant in the medium. The percentage germination was greater on the distilled water than on the nutrient salt cultures, being 40 per cent. in the former and 10 per cent. in the latter, but in the latter medium there were a few exceedingly large protocorms up to 4 mm. in length.

The addition of 1 per cent. dextrose to the nutrient salt medium obviously produced a condition which upset the delicate balance of fungus and host. Infected embryos became parasitised. In some instances this happened before any growth of the embryo had taken place, but in others considerable initial growth had been attained before the meristematic tissues were finally invaded by the hyphae.

Where the medium consisted of 50 per cent. nutrient salt solution, 50 per cent. potato extract and 1 per cent. dextrose a more stable condition again prevailed. Germination occurred in about 75 per cent. of the seed and the protocorms, averaging 1 mm. in length; all contained the endophytic fungus. One or two embryos were completely parasitised by the hyphae before any initial growth had been effected; all other non-stimulated embryos were without the endophyte. Of the experimental media this proved the most satisfactory for germination and growth in the presence of the smaller endophytic fungus.

Thus the slender species of *Rhizoctonia*, associated with the roots of *Listera ovata*, stimulates germination of the seed of this orchid on a medium consisting of water or basic nutrient salts and in the absence of carbohydrates or growth substances other than the traces of these materials present in agar. To attain a higher percentage germination a balanced medium containing carbohydrates, nutrient salts, and growth substances is probably necessary, as evidenced by the germination results on nutrient salts plus potato extract plus dextrose.

B. *Large Endophytic Fungus.*—This endophytic fungus, while growing more freely than the smaller species on all the experimental media, did not stimulate germination in any of the cultures. On sugar-free media the large majority of embryos were not penetrated by the hyphae and the few that were showed complete hyphal invasions of all the cells. On the other hand, cell enlargement in non-meristematic regions of the embryo occurred more frequently in these cultures than in the control tubes or those with the smaller species. The significance of this cell enlargement is as yet unknown.

On media containing sugar, the growth of the mycelium was so great that the seeds were deeply embedded in the fungal mat and details of embryo structure could not be ascertained.

The two species of *Rhizoctonia*, occurring as mycorrhiza in the roots of the adult plant, differ very greatly in their effect on germination. The smaller can stimulate germination in water or on a balanced substrate, while the larger species does not activate growth of the embryos, as evidenced in the experimental culture media.

SUMMARY.

1. The seed of *Listera ovata* will not germinate in water nor in nutrient salt solution in the absence of a symbiotic fungus.

2. The addition of dextrose and potato extract to a basic nutrient solution does not stimulate asymbiotic germination.

3. Two species of *Rhizoctonia* form mycorrhizal associations with the roots of adult plants of *L. ovata.*

4. The smaller species stimulates germination of the seed on distilled water agar; the larger species does not activate the growth of the embryo on any of the experimental media which were used.

NOTES ON THE OCCURRENCE OF TWO RARE UREDINEAE.

By D. G. DOWNIE, Ph.D.

1. *Uromyces Acetosae* Schröt.—While *Uromyces Acetosae* has been observed on *Rumex acetosa* in many different localities in Scotland, the occurrence of the aecidia appears to be rather a rare phenomenon. Wilson (1934) records two collections of the aecidial stage in Scotland, one by W. Evans on the Isle of May, 1912, and the other at Inverliever, Argyllshire, in May 1923. Miss F. Greig of the Department of Botany, University of Aberdeen, collected specimens of *Rumex acetosa* near Loch Lee, Forfarshire, on 13th June 1949, which, on examination, were seen to carry four spore stages of the rust *Uromyces Acetosae.* Aecidial sori were present on both leaf-blade and petiole in conspicuous purplish-red areas, which also carried a few spermagonia. The aecidia are amphigenous, small, cup-shaped, with a yellow pseudoperidium becoming paler at the revolute margin and containing bright yellow aecidiospores. The uredospore sori are also amphigenous and scattered over the surface of the leaf, often occurring on the same purplish-red areas bearing the aecidia. The uredospores are finely and densely verruculose with three germ spores. These characteristic features of the aecidia and uredospores were sufficient to determine the species, but the finding of a few teleutospore sori on one of the leaf petioles confirmed the diagnosis. The sori were dark brown, almost black in colour, teleutospores subglubose and minutely warted.

2. *Puccinia Polygoni-vivipari* Karst.—Specimens of *Polygonum viviparum* affected with *Puccinia Polygoni-vivipari* were collected by Miss Greig in Glen Muick, near Ballater, on 12th July 1949. Uredospore sori, light brown in colour, and surrounded by raised epidermis, were scattered over the lower surface of the leaf. Uredospore almost round and very finely echinulate. Teleutosporesori were more numerous, hypophyllous and dark brown in colour. The spores were obovate-oblong, rounded, not thickened above, and their average measurement was $23\,\mu \times 16\,\mu$. Wilson (1934) records that this rust has been found at Mar Lodge and Braemar in Aberdeenshire.

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A CONTRIBUTION TO OUR KNOWLEDGE OF THE FLORA OF THE ISLES OF LEWIS, HARRIS, KILLEGRAY AND ENSAY. By J. W. HESLOP HARRISON, D.Sc., F.R.S., and J. HESLOP HARRISON, M.Sc., Ph.D.

(Read by title, 20th January 1949.)

In 1939, in order to extend our knowledge of the flora of the Outer Hebrides, one of our parties worked the Uig district of Lewis as well as the adjacent islands of Great Bernera and Little Bernera. As a result two papers were published: (1) "Botanical Investigations in the Hebrides" (Proc. King's College Agric. Students' Assoc., vi, December 1939), by Helena Heslop Harrison, providing a few references to the rarer plants; and (2) "Noteworthy Plants from Great and Little Bernera (Lewis), Pabbay and Berneray (Harris), and the Uig District of Lewis" (Proc. Univ. Durham Phil. Soc., x, 214–221, 1939), by W. A. Clark and J. Heslop Harrison, containing a complete list of the more important plants collected in the areas mentioned. Later, in 1941, we published a "Preliminary Flora of the Outer Hebrides" (Proc. Univ. Durham Phil. Soc., x, 228–273) in which all the plants discovered in the Uig district, common and rare alike, were set out.

These three papers supplied the first accounts of the Uig flora ever published, and it is significant that recent work has done but little to extend them.

Immediately after the publication of our "Preliminary Flora" in 1941, we were able to spend a month on the Isle of Harris, a period devoted chiefly to a study of the plants growing on North Harris and on the adjoining portions of South Harris. An account of our investigations appeared in the Journal of Botany (lxxix, 164–169, 1941) under the title "Observations on the Flora of the Isle of Harris (v.c. 110)."

From the above facts it will be clear that much of Lewis and Harris, in addition to some of the islands in the Sound of Harris, remained to be explored. During 1948 and 1949, in order to remedy these defects, expeditions were organized to work the western portions of Lewis from the Butt to Callanish, the coasts on all sides of Stornoway, the southern areas of South Harris and the Isles of Killegray and Ensay. In all cases, whenever possible, the adjoining mountains and moorlands were also examined. The more interesting results of these researches are embodied in the present paper, but, for biogeographical reasons, it has been considered proper to provide an appendix detailing all the common plants found on Killegray and Ensay.

Concerning plants collected around Stornoway, a warning is imperative. Owing to the extensive plantations near the town, records from the Lews Castle grounds should be received with considerable caution. Many plants encountered there have undoubtedly been brought in when the woods were planted.

These introductory remarks would be incomplete without our tendering our heartiest thanks to Mr. and Mrs. L. H. Lomas of Kyles Lodge, Leverburgh; Col. and Mrs. Douglas Walker, Borve Lodge, Borve; Dr. P. A. MacLeod, Carloway; and Miss A. MacKenzie, North Tolsta, for their unstinted hospitality and help, and to the Research Committee, King's College, Newcastle-upon-Tyne, for their generous financial support.

Thalictrum arenarium Butcher.

Not uncommon on the dunes at North Tolsta, Coll, Gress, Barvas, Dalemore, Dalebeg, and Eoropie, Isle of Lewis; Borve, Horgabost, Northton, Isle of Harris; Isles of Killegray and Ensay.

T. montanum Wallr.

Barvas and Eoropie, Lewis, but not so plentiful as the preceding.

Ranunculus Drouetii F. Schultz.

In a pool and in drainage lodes, Eoropie, and at Shawbost, Lewis.

R. circinatus Sibth.

Not rare in a lochan on Ensay.

R. hederaceus L.

On muddy ground near Stornoway and Gress; also at several points down the west coast of Lewis.

R. reptans L.

In Loch Rahacleit and adjacent lochans, Lewis.

R. bulbosus L.

On the dunes, Killegray.

R. Ficaria L.

Common in the Lews Castle grounds, at the base of cliffs near Kirivick and Carloway, and on Ben Bragor, Lewis; not rare in the Harris gorges and extremely abundant on the Isles of Stromay, Saghay Beg, Saghay More, Killegray and Ensay, in the Sound of Harris.

Caltha radicans T. F. Forst.

Although the more usual *C. palustris* L. occurs in most suitable places, much of the material from Eoropie to Callanish, from North Tolsta to Melbost on Lewis, and from various points in South Harris and the Isles in the Sound belongs to this segregate.

Nymphaea alba L.

Distinctly rare; only recorded from Loch Geiraha, north of Tolsta, in the east of Lewis, and from Loch Dalebeg in the west.

N. occidentalis (Ostenf.) Moss.

Irregularly distributed in Lewis and Harris, but not north of a line from Stornoway to Carloway.

Papaver dubium L.

In an oat field, Gress, Lewis; Northton, Borve, etc., Harris; and on Killegray.

Nasturtium officinale R. Br.

Common enough at Stornoway, Gress and Barvas, Lewis; in a stream near Loch Cistavat, S. Harris; on Killegray and Ensay. Many specimens were examined critically, but *N. uniseriatum* Howard & Manton was not encountered. So far that species has occurred only at Borve, S. Uist, in the Outer Isles.

Rorippa sylvestris (L.) Besser.

In some abundance around the mouth of the burn at Borve, S. Harris.

Cardamine flexuosa With.

If we accept the usual criteria for determining this species, plants referable to it were collected on the Carloway cliffs, Lewis, in stream gorges in S. Harris, and on the Isle of Ensay.

Erophila spathulata Lang.

Common on the sand dunes at Coll, Isle of Lewis.

Cochlearia officinalis L.

On Tolsta Head and at Dalemore, Lewis, also on Killegray and Ensay.

C. danica L.

Found sparingly on Saghay Beg and the sea-banks north of the dunes, Killegray.

C. scotica Dr.

Not uncommon from the Butt of Lewis to Brue, Lewis, and on Ensay.

Sisymbrium officinale Scop.

On waysides, Back and Barvas, Isle of Lewis.

Subularia aquatica L.

Quite common on Lochs Rahacleit, Eilaster, Almaistean and other lochans near Carloway, and in Lochs Diridean and Langavat Mor between North Tolsta and Muirnag, Lewis.

Coronopus squamatus (Forsk.) Aschers.

A weed around a croft in Glen Horgabost, S. Harris.

Cakile maritima Scop.

Not common on Lewis near Melbost, Dalemore and Barvas; Horgabost, Harris; plentiful on Ensay, but much rarer on Killegray; all of the examples collected were examined critically in case *C. edentula* Hook. turned up.

Raphanus maritimus Sm.

Sparingly on the dunes at Northton, S. Harris.

Viola palustris L.

As we have not been able to record the marsh violet from the neighbouring Isles of Berneray and Pabbay (Sound of Harris), the presence of the species on Ensay seems worthy of note.

V. Lloydii Jord.

On cultivated land at Stornoway, North Tolsta, Swanibost and Carloway, Lewis; and at Borve, S. Harris.

V. arvensis L.

The segregates *V. segetalis* Jord. and *V. obtusifolia* Jord. were obtained from sandy fields, Northton, S. Harris.

V. Curtisii E. Forst.

On all the machair land in S. Harris and Killegray.

Polygala serpyllifolia Hose.

Whilst the usual forms seemed well distributed in appropriate habitats, the var. *vincoides* of this species occurred only on the dunes at North Tolsta, Lewis.

Silene maritima With.

Abundant on the Butt of Lewis, cliffs near Carloway and Dalebeg and on Tolsta Head, as well as on shingle at Brue and Barvas, Lewis; on Toe Head, S. Harris.

Melandrium album (Mill.) Garcke.

Sparingly around Ensay House, Ensay; also with pink flowers, not the result of hybridity with *M. rubrum*, at Borvemore, S. Harris.

Cerastium semidecandrum L.

Not rare, but very variable, on sandy ground from Eoropie and North Galston to Shawbost, Lewis.

Arenaria serpyllifolia L.

On dunes and in dune slacks everywhere, but not in great quantities. A very well-marked form of the segregate *A. Lloydii* Jord. was collected on the Isle of Killegray.

Sagina nodosa (L.) Fenzl.

Not rare, in company with *Carex maritima*, on the area between Barvas sand dunes and the loch, Lewis; very common at Northton, S. Harris, and on Killegray and Ensay.

S. maritima Sm.

Throughout the coastal areas examined, including those on Killegray and Ensay.

S. subulata Sw. (C. Presl.).

Occasional on moorland paths and on Ben Rahacleit, Lewis.

Spergularia salina Presl.

On marshy ground near the sea, Northton, S. Harris.

S. marginata (DC.) Kittel.

Sparingly on Traigh Luskentyre, S. Harris.

Hypericum pulchrum L.

Thinly distributed in the hilly areas around Callanish and Carloway, Lewis, and in S. Harris; the peculiar Atlantic island form var. *procumbens* Rost. was found on Ben Bragor, in ravines on S. Harris, and on Killegray and Ensay.

Radiola Linoides Roth.

Growing amongst Calluna, etc., on an almost perpendicular bank at North Galson, and by the roadside at Arnol, Lewis.

Geranium sylvaticum L.

Once only, in the Lews Castle grounds, Stornoway.

G. molle L.

Sparingly on the Gress dunes, but much more frequent on dune and machair from Eoropie to Callanish, Lewis, and from Horgabost to Northton, S. Harris; also on the Isle of Killegray.

G. pusillum L.

Around the farm buildings on Killegray.

G. dissectum L.

Rare on sandy ground lying fallow at Borve and Northton, S. Harris.

Erodium cicutarium L'Herit.

Not rare on sands and machair, N. Tolsta, Coll, Gress and Barvas, Lewis; also at Borve and Northton, S. Harris, and on Ensay and Killegray. In the latter island white-flowered plants occurred freely.

Oxalis Acetosella L.

Abundant in the Stornoway woods, but not as common amongst rocks, Kirivick, Lewis; cliffs above Slettnish, Isle of Scarp, and below Husival Mor and Husival Beg, N. Harris; not rare in the ravines on S. Harris.

Ilex Aquifolium L.

Odd examples on Griosamol, Lewis.

Ulex europaeus L.

Here and there around Stornoway, Callanish, etc., Lewis, and between Loch Langavat and Leverburgh, S. Harris; in all probability planted.

Sarothamnus scoparius (L.) Koch.

Near Balallan, Isle of Lewis; no doubt introduced.

Ononis repens L.

Plentiful at one point, Isle of Ensay; the second Outer Hebridean station.

Medicago sativa L.

On the machair at Borve, S. Harris; doubtless the relics of past cultivation.

M. lupulina L.

One station near Leverburgh, S. Harris.

Trifolium medium L.

Rare on the cliffs at Kirivick and Dalemore, Lewis.

T. dubium Sibth.

Not uncommon near Stornoway, but much rarer at Borve and Barvas, Lewis; also at Leverburgh, S. Harris.

Vicia sepium L.

Local near Stornoway, Coll, North Tolsta, Callanish, Carloway, and Barvas, Lewis; in some quantity west of Rodel, Harris; and on the Isle of Ensay.

V. sylvatica L.

On cliffs between Slettnish and Rudha Ruadh, Isle of Scarp, N. Harris.

Lotus uliginosus Schkuhr.

Amongst rushes in a field south of the Stornoway woods, Lewis.

Lathyrus pratensis L.

Between Tolsta and the sea in the east of Lewis, and of occasional occurrence in the west from North Galson to Dun Carloway; in coastal areas, S. Harris; and on Ensay.

L. montanus Bernh.

On the cliffs just south of Stornoway, Carloway and Dalemore, Lewis; in Glen Seilebost, S. Harris.

Filipendula Ulmaria (L.) Maxim.

Common locally at N. Tolsta, and from Shawbost to Loch an Duin, Dun Carloway, Lewis; not at all rare in the west of S. Harris and on Killegray and Ensay.

Rubus idaeus L.

In the little woodland at Borve, S. Harris.

R. saxatilis L.

One large clump on Chaipaval, S. Harris; on the cliffs behind the village, Isle of Scarp.

Fragaria vesca L.

In great abundance on some of the bank sides in the woods near Stornoway.

Comarum palustre L.

Near Coll and here and there between South Dell and Callanish, Lewis; the Bull Ring, Horgabost, S. Harris; and on Killegray and Ensay.

Alchemilla glabra Neygenfind.

Common in a gorge on Chaipaval, S. Harris.

Rosa canina L.

An endemic form, different from, but clearly allied to, var. *viridicata* Rouy grows on a cliff ledge on the Isle of Killegray whilst a second form close to var. *biserrata* Mer. was collected on the cliffs near Kirivick and Carloway Harbour. Forms best referred to vars. *lutetiana* Lem. and *sphaerica* Gren. occur at Fincastle, Horgabost, and in Glen Seilebost, Harris; and on the cliffs of Ben Bragor and Dalemore, Lewis. Toward the top of Bulaval, Harris, the variety *spuria* sprawls over the rocks.

R. dumalis Bechs.

As it is practically certain that this is the *Rosa glauca* of most authors, and as the name antidates *R. afzeliana* Fr., it is employed here. In Lewis var. *glaucophylla* (Winch) H.-Harr. was obtained fairly freely along the Coll river and on the cliffs at Carloway and Dalemore; in South Harris it grew on the lower portions of the hill gorges. In the Lewis stations var. *adenophora* (Gren.) H.-Harr. also occurred, whilst in the Harris localities, as well as near Rodel, var. *Reuteri* (God.) H.-Harr. was not rare. Of some importance is the fact that in the *subcanina* series, f. *latifolia* (W.-Dod) H.-Harr., hitherto only reported from the Orkneys, may be found on rocks about Carloway Harbour.

R. mollis Sm.

This species is exceedingly rare in the Outer Hebrides, and in most cases its status seems doubtful. An anomalous form, with large subglabrous leaves, glandular above and below, occurs on the Dalemore cliffs, Lewis; a second, with small fruit, was collected high up the ravine sides on the Seilebost river, Lewis. Both of these are reserved for further study.

R. Sherardi Davies.

The form *pseudomollis* Ley was detected in the Stornoway woods and on the Kirivick and Carloway cliffs. This is undoubtedly the plant recorded from Carloway and Breasclete as *R. mollis* by M. S. Campbell (Report, B.E.C., xi, pt. 5, 1938). Copious gatherings, made by us over a wide area, and subjected to critical examination, uniformly contained this species and not *R. mollis*. Forms near the var. *omissa* Desegl., in addition to var. *pseudomollis*, occur on S. Harris where, at Kyles Lodge, var. *suberecta* (Ley) H.-Harr. may also be found. Further, a very curious plant, without fruit, growing in a gorge on Chaipaval will repay study.

Sorbus Aucuparia L.

In Stornoway woods, on islets in many sheets of water from Loch Roaoinavat to Loch Laxavat, on the cliffs of Ben Bragor, at Carloway and elsewhere in Lewis; in similar places in S. Harris, and on Ensay and Killegray.

Saxifraga stellaris L.

On the northern slopes of Roneval, and Mullach Buidhe, S. Harris; on Husival Mor and Husival Beag, N. Harris.

Chrysosplenium oppositifolium L.

Far from rare in the Castle woods, Stornoway.

Sedum rosea (L.) Scop.

On Tolsta Head, the Butt of Lewis, cliffs at Dalemore and Dalebeg, Lewis; on Roneval and Toe Head, S. Harris.

S. anglicum Huds.

On the Isles of Stromay and Saghay Beg.

S. acre L.

At Coll on the dunes, Lewis; in similar localities at Northton, Borve and Horgabost, S. Harris; also on Ensay and Killegray.

Drosera anglica Huds.

Never really common between Lochs Raoinavat and Laxavat, Lewis; on the moorlands of Harris more prevalent, but rare on Killegray.

D. longifolia L.

Northward of Roneval toward Loch Longavat and in the Meodale ravine, S. Harris; quite rare.

Hippuris vulgaris L.

In the lochan, and on marshy ground, Eoropie, around Loch na Cloich and an adjacent lochan west of N. Tolsta, Loch Risard, and the smaller loch near Loch Rahacleit east of Carloway. In two of these cases the plant was growing in pure sphagnum. In S. Harris the plant flourishes in the Northton marshes.

Myriophyllum spicatum L.

Only observed in the loch at Barvas, Lewis; and in Loch Cistavat, S. Harris.

M. alterniflorum DC.

In lochans from Finsbay to Loch Langavat, S. Harris.

Peplis Portula L.

On the roadside south of Barvas Post Office; very common in ditches at Lower Barvas, Brue, Dalebeg and Shawbost, Lewis.

Callitriche intermedia Hoffm.

Often, with Littorella, forming the sole occupants of lochs and lochans between Borve and Callanish, Lewis; also in S. Harris, and on Killegray and Ensay.

Conium maculatum L.

On waste ground, Barvas, Lewis.

Apium inundatum (L.) Rchb. f.

On Killegray and in the stream at Horgabost, S. Harris.

Aegopodium Podagraria L.

A pernicious weed everywhere from N. Tolsta to Stornoway and from North Galson to Callanish, Lewis; from Rodel to Borve, S. Harris, and on Ensay and Killegray.

Conopodium majus (Gouan) Loret & Barr.

In two fields south of the Castle woods, Stornoway, and on the Isle of Ensay; quite abundant.

Myrrhis Odorata (L.) Scop.

Near Barvas, Lewis, and no doubt an introduction.

Chaerophyllum temulum L.

Rare near Callanish and Barvas, Lewis.

Oenanthe crocata L.

On the Isle of Killegray; locally quite common.

Ligusticum scoticum L.

Tolsta Head, cliffs south of the Butt of Lewis, Dalemore and Dalebeg, Lewis; north of Borve, S. Harris, and Isle of Ensay.

Caucalis Anthriscus Huds.

On the top of a cliff west of Ensay House, Ensay.

Hedera Helix L.

Climbing up a cliff between Rodel and Leverburgh, S. Harris; on the cliffs behind the houses, Isle of Scarp.

Lonicera Periclymenum L.

On rocks along the Coll river in East Lewis, on Ben Bragor and many cliffs in the Carloway–Callanish area in the west; well distributed on rocks in S. Harris; and on sea cliffs, Ensay and Killegray. At Callanish a form was found with leaves 9·5 cm. long and 0·8–1·1 cm. wide.

Sherardia arvensis L.

Abundant on the machair, south of Borve Lodge, S. Harris.

Valeriana officinalis L.

On a cliff on the south bank of the Coll river, Lewis.

Valerianella locusta L.

On the dunes, Isle of Killegray.

Succisa pratensis Moench.

The dwarf, single-flowered, seacoast ecotype abounds on Nisabost Point, S. Harris.

Solidago Virgaurea L.

On cliffs and rocky loch margins from Dalebeg to Ben Bragor and Callanish, Lewis, in forms generally resembling the *S. cambrica* of Hudson. The same forms are widespread on S. Harris and on the Isle of Killegray.

Aster Tripolium L.

A very dwarf form of this species occurs in the salt-marsh at Gress, Lewis.

Antennaria dioica Gaertn.

One patch on Kirivick cliffs, and also on the Isle of Killegray. The subspecies *A. hyperborea* D. Don is common in the triangle Rodel–Roneval–Finsbury on S. Harris, even down to sea-level.

Inula Helenium L.

Only noted near Shawbost and Brue, Lewis; at Finsbay, S. Harris; and on Ensay.

Achillea Millefolium L.

Very plentiful, with the var. *lanata* Koch occasionally prevailing.

Chrysanthemum Leucanthemum L.

Rather rare, Dun Carloway, Melbost and Stornoway, Lewis; Borve, S. Harris.

Matricaria maritima L.

On Tolsta Head, Butt of Lewis, and on rocks, cliffs, and shingle elsewhere in Lewis and S. Harris.

M. matricarioides (Less.) Porter.

Common in many stations near crofts around the coasts of Lewis and Harris; also on Killegray and Ensay.

Tanacetum vulgare L.

Common around crofts at Back, Brue, Bragor, etc., Lewis; Borve, Northton, Rodel, etc., Harris; Ensay and Killegray.

Artemisia vulgaris L.

Throughout Lewis and Harris near crofts, and on the machair; also on the islands in the Sound of Harris.

Tussilago Farfara L.

In odd stations around Stornoway in the east, and from the Butt of Lewis to Brue in the west of Lewis; at Borve, S. Harris, and on Ensay.

Petasites hybridus (L.) G.M.S.

Very abundant in the east and west of Lewis along streams, and even, as at Barvas and Tolsta, on the dunes; locally plentiful on Ensay.

Arctium vulgare (Hill) A. H. Evans.

Often plentiful near habitations on Lewis and Harris.

Centaurea nemoralis Jord.

One collection, made at Horgabost, S. Harris, was composed of this species.

Centaurea obscura Jord.

Occurring on Lewis and S. Harris and in suitable localities as well as on Ensay and Killegray.

Hieracium Pilosella L.

Very local; only noted along the Coll river on Lewis, and on Killegray and Ensay.

Vaccinium Myrtillus L.

Not at all rare on the moorlands and in ravines on S. Harris, but only found near Stornoway, Loch na Cloich, and Loch Laxavat, Lewis; on Strone Udemul, Isle of Scarp; also on Killegray.

Arctostaphylos Uva-ursi (L.) Spreng.

In the Gill Meodale, Glen Seilebost, and Glen Dullin, S. Harris.

Erica Tetralix L.

This species shows an extensive range of variation on S. Harris, notably in leaf width, ciliation and in the posture of the upper leaves of the flowering stems. Examples occur in which the leaves are broad and flattened and practically glabrous above, and with the characteristic mealy down much reduced. In these forms the upper leaves of the flowering stems, which are normally closely adpressed, are spreading and conspicuous. In some respects, these plants are reminiscent of the curious forms of the species which occur in Donegal, and which have roused suspicion of ancient hybridity with *Erica mackaiana* Bab.

Primula vulgaris L.

Scattered but not rare; Gress, Coll, Stornoway, cliffs near the Butt of Lewis, Ben Bragor, Carloway, etc., Lewis; also on S. Harris, Ensay, Killegray, Saghay Mor and Saghay Beg. The undersides of the leaves are often very closely felted.

Anagallis tenella Murr.

Very local from North Galson to Callanish, Lewis, but frequent on Harris, Ensay and Killegray; in Ensay many plants with white flowers were observed.

Centunculus minimus L.

In several localities on Ensay.

Samolus Valerandi L.

On the edges of the marshes, Northton, S. Harris.

Lysimachia nemorum L.

In Stornoway woods.

Centaurium umbellatum Gilib.

From Seilebost to Scarasta, S. Harris; Isle of Ensay.

Gentiana baltica Murb.

In the west of Lewis and Harris generally distributed on machair land, with white-flowered forms at Horgabost, S. Harris; only on the Tolsta dunes in the east of either island.

G. amarella L.

Growing with *G. campestris* on the northern extremity of the Tolsta dunes.

Menyanthes trifoliata L.

Not common in lochs and lochans along the Stornoway–Barvas road, and in the Callanish–Carloway area; commoner in the S. Harris lochs, and not very rare on Ensay and Killegray.

Myosotis scorpioides L.

Very rare; only a few plants noted near Stornoway, Gress, and Port of Ness.

Symphytum officinale L.

Near Laxadale and Dun Carloway, Lewis; and on Ensay.

Calystegia sylvestris (Willd.) Roem & Schult.

Occurs as an escape near Leverburgh, S. Harris. The plant growing at Callanish, Lewis, is *C. sepium* L.

Convolvulus arvensis L.

Plentiful on reverting machair land near Borve, S. Harris.

Linaria Cymbalaria (L.) Mill.

Naturalized on walls in the Lews Castle grounds.

Digitalis purpurea L.

In the Lews Castle woods, Stornoway, not rare; a single plant near Callanish, Lewis.

Mimulus guttatus DC.

Very abundant from North Tolsta to Stornoway and from Eoropie to Callanish, Lewis; much rarer in the southern areas of S. Harris.

Sibthorpia europaea L.

In the grounds of the Lews Castle; obviously an escape from the derelict greenhouses where it has been employed as a substage plant and still persists.

Veronica serpyllifolia L.

Common in the Stornoway district, and near Rodel and Leverburgh, S. Harris.

V. scutellata L.

At Eoropie and Breasclete, Lewis; and on the Isles of Killegray and Ensay.

V. Anagallis-aquatica L.

Common enough at Gress and from Eoropie to Barvas, Lewis; at Borve, S. Harris: and on Killegray and Ensay.

V. Beccabunga L.

Plentiful along one stream, east of the road near Gress.

Utricularia minor L.

In moorland pools east of Muirnag, Lewis; on S. Harris, Ensay and Killegray.

Pinguicula lusitanica L.

Scattered on S. Harris; foot of Ben Rahacleit, near Lochs Laxavat, Raoinavat, etc., Lewis; occasionally on Ensay.

Mentha aquatica L.

Around Loch an Duin, Dun Carloway, Callanish, Lewis; Borve, S. Harris; Ensay and Killegray.

M. piperita L.

Introduced on Killegray.

M. Alopecuroides Hull.

In a ditch around a field below the Kirivick cliffs, Lewis; doubtless an escape.

M. arvensis L.

Very rare in fields in the southern portions of S. Harris.

Origanum vulgare L.

Rare in the grounds of the Lews Castle, Stornoway.

Scutellaria galericulata L.

Very sparingly on shingle, South Galson and Dun Carloway, Lewis.

S. minor Huds.

Behind a rocky knoll in the little valley, north of North Galson, around Loch Raoinavat, Loch Laxavat, along the Carloway river, on moorlands near Ben Bragor and Muirnag, Lewis; Glen Horgabost, Loch Langavat, S. Harris; and on Ensay and Killegray.

Stachys palustris L.

Very local at Back, North Tolsta, Port of Ness, Shawbost, Dun Carloway, and Callanish, Lewis; Northton, S. Harris.

The hybrid *S. palustris* × *S. sylvatica* occurs in the latter station.

S. arvensis L.

As a weed at Callanish.

Teucrium Scorodonia L.

Common on cliffs at Fincastle, between Rodel and Kyles Lodge, and in Glen Seilebost, S. Harris, as well as on cliffs on Husival Beag, N. Harris.

Ajuga reptans L.

Plentiful in the Lews Castle woods, Stornoway.

Salicornia stricta Dum.

In the salt-marshes at Coll, Lewis; Northton and Traigh Luskentyre, S. Harris.

Polygonum amphibium L.

Common in Loch Branahuie and on wet ground near Eoropie, Barvas, etc., Lewis; lochan near Rodel, Harris; also on Killegray and Ensay.

P. viviparum L.

First recorded by us from sea-level stations on Little Bernera, and Uig, Lewis, in 1939; now reported from cliffs behind Loch na Learg and on Strone Udemul, Isle of Scarp; also from Husival Mor, N. Harris.

Oxyria digyna (L.) Hill.

On Husival Mor, N. Harris.

Euphorbia Helioscopia L.

Amongst oats near Brue and Shawbost, Lewis; and on Killegray.

E. exigua L.

Odd specimens on abandoned ground near Borve, S. Harris.

Urtica urens L.

Not rare in waste places on the west coast of Lewis; likewise near the houses on Killegray and Ensay.

Betula pubescens Ehrh.

Whilst much of the material examined from the Outer Hebrides belongs to this aggregate, in our opinion the segregate concerned in Harris and S. Uist is *B. tortuosa* Led.

B. pendula Roth.

In the little wood near Borve, S. Harris.

Corylus Avellana L.

On the cliffs of Ben Bragor and at Dalemore, Carloway, and Kirivick on Lewis; on S. Harris from Rodel to Leverburgh and in Glen Seilebost; also amongst rocks behind the village, Isle of Scarp.

Salix aurita L.

Common near Stornoway, South Shawbost and southward to Callanish and Breasclete, but not found north of the Geiraha–North Galson line; abundant in S. Harris, Killegray, and Ensay.

S. Caprea L.

In the Castle woods, Stornoway; not rare.

S. atrocinerea Brot.

Plentiful on islets in Loch Laxavat and around the shores of Loch Eilaster and other lochans in the Carloway area of Lewis, also near Breasclete; in all the mountain gorges in the west of S. Harris.

S. atrocinerea × *S. aurita.*

In the Meodale ravine, S. Harris.

S. nigricans Sm.

Likewise found in its typical guise in the Castle grounds. In Lewis, and elsewhere in the Outer Hebrides, there is to be found a willow, often planted, but possibly native in some of its stations, which Wilmott has labelled *S. nigricans* var. *hebridensis.* This plant cannot be distinguished from certain Tynedale specimens which, despite their slight pubescence, can only be regarded as appertaining to *S. phylicifolia.* There seems no reason, therefore, for taking up Wilmott's alleged new *nigricans* variety. The plant may be observed planted around many crofts in Western Lewis, as well as in Harris.

S. phylicifolia L.

A single shrub growing over a rock along the Abhainn Gillan Tailleir, S. Harris.

S. repens L.

Locally common as an aggregate, both in Lewis and Harris, but the segregate, *S. arenaria* L., is not uncommon on machair land as well as in Ensay and Killegray.

S. repens × *S. aurita.*

This hybrid occurred at Coll and Carloway in Lewis; it was encountered not infrequently in Harris, where, along the stream flowing along Glen Horgabost, it displayed great variation, no doubt originating in F_2 generations and back crosses.

S. herbacea L.

On Ben Bragor and Ben Rahacleit, Lewis, where also occurred a long-leaved form; and on Husival Mor and Beidig, N. Harris.

Populus tremula L.

In Lewis, on cliffs on Ben Rahacleit, near South Shawbost, Dalemore, Dalebeg, Kirivick and Carloway, also on islets in lochs like Loch Laxavat; in S. Harris at Borve, Loch na Moracha, on Bulaval and in all rocky gorges; also on a cliff ledge on Killegray.

Empetrum nigrum L.

Very rare on the moorlands north of the Grundale Burn, Mid-Borve; more plentiful around Loch na Cloich, Tolsta in East Lewis, near Loch Raoinavat, and thence to Loch Eilaster in the Carloway district; widely distributed on the moors of S. Harris, Ensay, and Killegray.

Hammarbya paludosa (L.) O. Kuntze.

Rare on the Toe Head side of Chaipaval, S. Harris; behind Rudha Ruadh, Isle of Scarp.

Listera ovata R. Br.

Not rare between North Tolsta and the Traigh Mhor, and at Barvas, Lewis; on machair and fixed dune at Borve, Seilebost, Horgabost and Northton, S. Harris.

L. cordata R. Br.

Under overhanging heathery banks around Loch na Cloich, N. Tolsta, Lewis; in the Red Gill leading to Loch Cravadale, Harris.

Orchis latifolia L. sec. Pugsley.

This orchid occurs everywhere in the coastal zones of Lewis from North Tolsta to Melbost, and from just south of the Butt to Callanish and Breasclete. As a general rule, var. *coccinea* Pugl. prevails, but it should be emphasized that near Breasclete quite typical forms are common. Moreover, on the flats near the Coll salt-marsh a magnificent new form, obviously having some near relationship with *O. majalis* Reichb., flourishes. This is now being subjected to statistical analysis by J. Heslop Harrison. The var. *coccinea* abounds on the machairs of S. Harris as well as on Killegray and Ensay.

O. purpurella T. & T. A. Steph.

This species flourishes in precisely the same areas as the preceding, but, as it is more tolerant of lower pH values, it proceeds further inland, and also along the south coast of Harris. Mixed colonies, exhibiting but few traces of hybridization, exist. Behind the dunes at Barvas, Lewis, and along the stream ending blindly there, huge forms, more closely approximating to *O. majalis* than to Durham *O. purpurella*, occur in great numbers. These plants are being included in the same critical survey as *O. latifolia*. The species is common on S. Harris, Killegray, Saghay Mor, and Ensay.

×*O. viridella* J. Heslop Harrison (= *O. purpurella* × *Coeloglossum viride*).

On the machair south of Borve, S. Harris.

O. Fuchsii Dr.

Of this species the var. *hebridensis* (Wilm.) H.-Harr. is locally abundant. Nevertheless, very strange gaps exist in its distribution. At North Tolsta and Coll, on Lewis, it swarms and then thins out rapidly southward. In the west it prevails near Eoropie, Swanibost and Lionel, only to fail completely until the Berie sands are reached when it again becomes plentiful. The plant is widespread in the Luskentyre district of S. Harris, especially in the little wood.

The extraordinary tendency of this species to develop highly fertile hybrid swarms with *O. purpurella* seems remarkable when cognizance is taken of the fact that in *O. Fuchsii* var. *hebridensis* the chromosome number is 40 and in *O. purpurella* 80. Apparently, some form of double fertilization is responsible for the phenomenon. Such hybrid swarms exist near Tolsta and in the Habost and Loch Stiapavat district, Lewis. This proclivity should be contrasted with the exceedingly great difficulty *O. Fuchsii* var. *hebridensis* finds in producing crosses with *O. latifolia*. Thus, on the sands at Eoropie, where *O. latifolia* ($2n = 40$) and *O. Fuchsii* var. *hebridensis* grow intermingled in enormous quantities, only two plants of the parentage *O. latifolia* × *O. Fuchsii* var. *hebridensis* (= ×*variabilis* H.-Harr.) were detected. On the other hand, as one approaches Loch Stiapavat, where *O. latifolia* vanishes to be replaced by *O. purpurella*, the population includes great numbers of *O. purpurella* × *O. Fuchsii* var. *hebridensis*, exhibiting a noteworthy degree of uniformity in facies.

O. ericetorum (E. F. Linton) E. S. Marshall.

Quite common on the moorlands of Lewis, Harris, Killegray, and Ensay. This species ($2n = 80$) likewise produces hybrid swarms with *O. purpurella* with great facility, and such occur at Borve, Northton, Harris; Back, Coll, Gress, Dalebeg and Callanish, Lewis; as well as on Killegray. Curiously enough, despite the disparity in chromosome numbers, hybrid swarms are developed to a limited extent between it and *O. latifolia*, where the dunes merge into the moorlands at Borve, and on the lower slopes of Chaipaval, S. Harris.

Coeloglossum viride (L.) Hartm.

Often common; on sandy soil near North Tolsta, Melbost, Barvas and Dalemore, Lewis; also at Northton, Borve, Horgabost, and Seilebost, Harris; and on Ensay and Killegray. At Seilebost, many of the plants were very well grown, some attaining a height of 21 cm., with a spike of 8 cm. carrying 32 flowers.

Platanthera chlorantha (Cust.) Rchb.

In great abundance on swampy ground, Borvemore, and near Loch an Duin, S. Harris.

P. bifolia (L.) L. C. Rich.

Much less common, Borve, S. Harris.

Allium ursinum L.

One strong colony exists in the Castle woods, Stornoway.

Scilla non-scripta (L.) Hoffmgg. & Link.

Also in the Castle woods.

Juncus balticus Willd.

Local on bare sandy ground behind the dunes at Eoropie and Barvas, Lewis.

J. acutiflorus Ehrh. × *J. articulatus* L.

About Loch Gleann na Moine and Horgabost, S. Harris; Loch an Duin and Loch Almaistean in the Carloway district, Lewis.

Luzula sylvatica Gaud.

On lower cliffs along the Coll river, in Stornoway woods, on Ben Bragor, on the cliffs near Loch Raoinavat, Lewis; in similar places and ravines on S. Harris, but forming a close pure sward at many points between the summit of Chaipaval and Toe Head.

Typha latifolia L.

This forms a very interesting addition to the flora of the Outer Hebrides. A strong colony was discovered, on 29th June 1948, in the stream flowing into Loch a'Bhaile, Shawbost, at its north-west angle. Subsequently, a second station was noted just south of the Bragor–Shawbost road, which, at this point, runs almost due east and west.

Sparganium erectum L.

Far from rare at Callanish and on the stream behind the Barvas dunes, Lewis.

S. angustifolium Michx.

In several lochs near N. Tolsta and in others between Loch Barvas More to Breasclete, Lewis; also in Loch Langavat, Loch an Duin, S. Harris; lochan on the Isle of Scarp; and on Ensay.

Lemna minor L.

Locally plentiful on Killegray and Ensay.

Potamogeton natans L.

In the lochan at Eoropie and, sporadically, in the lochs and streams southward on Lewis; in similar habitats on Harris, Ensay, and Killegray.

P. gramineus L.

In the Barvas river just before it enters Loch Barvas More, Loch Dalebeg, Loch Risard and other lochans just west of Ben Rahacleit, Lewis; Loch Cistavat and Loch an Duin, S. Harris. A remarkable land form, with internodes greatly reduced, and short, broad, thick, roundish leaves was collected around Loch Dalebeg and along the Barvas river in 1949.

× *P. nitens* Weber.

In Loch Risard and Loch Cistavat.

P. alpinus Balb.

In plenty in the runnel running from Loch Stiapavat to Ness, two miles from the Butt of Lewis.

P. perfoliatus L.

In Loch Barvas More, Loch Ereray, Loch Shawbost, Loch Langavat, Loch Risard (with adjacent lochans), and Loch an Duin, Lewis; Loch Cistavat, S. Harris.

P. pusillus L.

Found only in Loch Eilaster, Lewis.

P. Millardii H.-Harr. (= *P. Berchtoldii* Dandy & Taylor non Fieber).

In dense masses in the stream draining Loch Stiapavat, near the Butt of Lewis.

P. filiformis Pers.

Abundant at the north end of Loch Cistavat, S. Harris.

× *P. suecicus* Richt.

Sparingly in Loch Cistavat.

P. pectinatus L.

In enormous masses in the pools of the Coll salt-marsh, Lewis; not common in Loch Cistavat, S. Harris.

Zostera marina L.

Abundant amongst the isles in the Sound of Harris.

Eleocharis uniglumis Schult.

In the marshes at Northton, S. Harris; and on Killegray.

Scirpus setaceus L.

At Borve, S. Harris; and on Ensay.

S. Tabernaemontani C. C. Gmel.

Abundant in one of the streams traversing the Coll salt-marsh, Lewis; in Loch Laxdale and lochans near Finsbay, S. Harris.

Blymus rufus (Huds.) Link.

In the salt-marsh at Callanish, Lewis.

Eriophorum latifolium Hoppe.

On the west shore of Loch na Cloich, N. Tolsta, Lewis.

Schoenus nigricans L.

Frequent and ascending high up the cliffs of Ben Bragor.

Rhyncospora alba (L.) Vahl.

Between Lochs Laxavat and Almaistean, Lewis; rare near Loch Gleann na Moine but more plentiful around Loch Allityer, S. Harris.

Carex dioica L.

Thinly distributed on the moorlands, Lewis and S. Harris.

C. maritima Gunn.

Excessively abundant on inundated areas behind the Eoropie and Barvas dunes; in the latter locality the ground was brown with fallen fruits; also common in similar stations at Northton and Scarasta, S. Harris.

C. disticha Huds.

This interesting sedge, new to the Outer Hebrides, formed mixed colonies with *C. maritima* at Barvas; not rare there.

C. Otrubae Podf.

Only on the Isle of Ensay and there restricted to a little hollow on the south coast.

C. Bigelowii Torr.

On Strone Romul, Isle of Scarp.

C. juncella Fr.

On the moorland, north-west of Roneval, S. Harris.

C. Hostiana DC.

Not common on Ben Bragor, and cliffs at Dun Carloway and Dalemore, Lewis; also on Killegray.

Phalaris arundinacea L.

At several points in Upper Barvas and along the Torray river, Lewis; Luskentyre, S. Harris.

Alopecurus pratensis L.

In fields at North Tolsta, Eoropie, and Callanish, Lewis.

Phleum pratense L.

Odd plants near Rodel, Kyles Lodge, and Borve, Harris.

Deschampsia caespitosa (L.) Beauv.

Not common, Rodel, Finsbay, etc., S. Harris.

D. setacea (Huds.) Hack.

Occasionally in watery places from Callanish to Dun Carloway, Lewis; in lochans in the Horsaclett district, S. Harris.

Helictotrichon pubescens (Huds.) Pilg.

Not rare near the sea on Lewis, Harris, Ensay, and Killegray.

Catabrosa aquatica (L.) Beauv.

Very common at stream mouths, North Tolsta, Coll, Gress, Barvas, Eoropie, North Galson, etc., Lewis; Northton, Borve, Horgabost, S. Harris; Ensay and Killegray.

Briza media L.

On the flats between Northton, S. Harris, and the sea.

Poa Chaixi Vill.

Common in one section of the Castle woods, Stornoway, south-west of the lawn.

Puccinellia maritima (Huds.) Parl.

In the salt-marsh at Breasclete and Callanish, Lewis; Crago and Northton, S. Harris; Killegray and Ensay.

Desmazeria loliacea (Huds.) Nym.

On the dunes at North Tolsta, Barvas, and Dalemore, Lewis; also on a sandy spit on the south shore of Killegray.

Bromus secalinus L.

One plant in Stornoway.

Brachypodium sylvaticum (Huds.) Beauv.

In a little ravine off the Luskentyre road, S. Harris.

Juniperus sibirica Burgsd.

On rocks behind Carloway, Lewis; plentiful in the S. Harris mountains, but thinning out westward; also scattered on the Isle of Scarp.

J. communis L.

Fairly common inland from Finsbay, S. Harris.

Ophioglossum vulgatum L.

Common behind the dunes at Eoropie and Barvas, Lewis; Seilebost and Northton, Harris; also on Ensay and Killegray.

Botrychium Lunaria Sw.

Scarce near North Tolsta, Coll, and Melbost, Lewis; also on the Isle of Stromay.

Osmunda regalis L.

On islets in Loch Fasgro, Loch Raoinavat, Loch Laxavat, and on the west shore of Loch an Duin, Dun Carloway, Lewis; in Glen Seilebost and along the sea-coast west of Kyles Lodge, S. Harris.

Hymenophyllum peltatum (Poir.) Desv.

On the summits of Ben Bragor and Ben Rahacleit, Lewis; in ravines on the lower slopes of Roneval, in the Meodale ravine and Glen Seilebost, S. Harris, and not rare on the Isle of Scarp.

Phyllitis Scolopendrium (L.) Newm.

As the var. *cristatum* on rocks above Loch Laxdale, S. Harris, collected by Mrs. Douglas Walker; also amid boulders, Gresclett, Loch na Cleavag, N. Harris.

Asplenium marinum L.

Found as a very luxuriant form on the Isle of Killegray.

A. Trichomanes L.

On Ben Bragor, Lewis; and Fincastle, S. Harris.

A. adiantum-nigrum L.

Sparingly in the gorges of S. Harris.

A. Ruta-muraria L.

On the cliffs at Kirivick, Lewis; Glen Seilebost, S. Harris.

Dryopteris paleacea Don.

This well-marked plant, differing generally and in its degree of polyploidy from *D. filix-mas*, is common enough in the hill gorges of S. Harris.

D. aemula (Ait.) O. Kuntze.

On a cliff at the head of the Seilebost ravine, S. Harris.

Thelypteris Oreopteris (Ehrh.) C. Chr.

Rare on Ben Bragor, Lewis, and in the Meodale gorge, S. Harris.

T. Phegopteris (L.) Slosson.

Not rare at the base of rocks in Glen Seilebost, S. Harris.

Polypodium vulgare L.

Generally distributed in suitable places; common on walls, Port of Ness.

Equisetum sylvaticum L.

Along the Coll river, Carloway, Callanish, Dun Carloway, Lewis; on the cliffs at Stettnish, Isle of Scarp.

E. variegatum Weber & Mohr.

Sand-flats, Barvas, Lewis: sand dunes, Isle of Ensay.

Lycopodium Selago L.

On Ben Bragor, Lewis; widespread on high ground in the west of Scarp.

Selaginella selaginoides (L.) Link.

Thinly distributed from North Galson in Lewis to the islands in the Sound of Harris.

Isoetes lacustris L.

In lochs between N. Tolsta and Muirnag, Loch Eilaster, Loch Almaistean, Lewis.

APPENDIX.

The Common Plants of Killegray and Ensay.

Ranunculus Flammula L.
R. acris L.
R. repens L.
Caltha palustris L.
Cardamine pratensis L.
Capsella Bursa-pastoris L.
Raphanus Raphanistrum L.
Viola Riviniana Reichb.
Polygala dubia Bellynck.
Lychnis Flos-cuculi L.
Cerastium tetrandrum Curt.
C. viscosum L.
C. vulgatum L.
Stellaria media Vill.
**S. uliginosa* Murr.
Arenaria peploides L.
Sagina procumbens L.
Spergularia sativa Boenn.
Montia fontana L.
Linum catharticum L.
Trifolium pratense L.
T. repens L.
Anthyllis Vulneraria L.
Lotus corniculatus L.
**Vicia Cracca* L.
Potentilla erecta L.
P. Anserina L.
Drosera rotundifolia L.
Callitriche stagnalis Scop.
Epilobium parviflorum Schreb.
E. obscurum Schreb.
E. palustre L.
Hydrocotyle vulgaris L.
Angelica sylvestris L.
Heracleum Sphondylium L.
Daucus Carota L.
Galium verum L.
G. saxatile L.
G. palustre L.
G. Aparine L.
Succisa pratensis Moench.
Bellis perennis L.
Gnaphalium uliginosum L.
**Achillea Ptarmica* L.
Senecio vulgaris L.
S. Jacobaea L.
Cirsium lanceolatum (L.) Scop.
C. arvense (L.) Scop.
Crepis capillaris Wallr.
Hypochaeris radicata L.
Leontodon autumnale L.
Taraxacum vulgare Schrank.
†*T. laevigatum* DC.
Sonchus oleraceus L.
†*S. asper* Hill
Calluna vulgaris (L.) Hull.
Erica Tetralix L.
E. cinerea L.
Glaux maritima L.
Gentiana campestris L.
Myosotis caespitosa Schultz
M. arvensis Hill
M. versicolor Sm.
Veronica arvensis L.

An asterisk denotes that the plant is found on Ensay only and a dagger on Killegray only.

Euphrasia micrantha Reich.
E. nemorosa Lohr.
E. confusa Pugsl.
Bartsia Odontites Huds.
Pedicularis palustris L.
P. sylvatica L.
Rhinanthus stenophyllus Schur.
Pinguicula vulgaris L.
Thymus Serpyllum L.
Prunella vulgaris L.
Galeopsis Tetrahit L.
**Lamium amplexicaule*
**L. mollucellifolium* Fr.
L. purpureum L.
Plantago Coronopus L.
P. maritima L.
P. lanceolata L.
P. major L.
Atriplex glabriuscula Edmonds.
Polygonum Persicaria L.
Rumex obtusifolius L.
R. crispus L.
R. Acetosa L.
R. Acetosella L.
Urtica dioica L.
Iris Pseudacorus L.
Narthecium ossifragum Huds.
**Juncus bufonius* L.
J. squarrosus L.
J. Gerardi Lois
J. conglomeratus
J. bulbosus L.
J. articulatus L.
Luzula campestris DC.
L. multiflora DC.
Triglochin palustre L.
T. maritimum L.
Potamogeton polygonifolius Pourr.
Eleocharis palustris Roem. & Schult.
E. multicaulis Sm.
Scirpus pauciflorus Lightf.
S. caespitosus L.
S. fluitans L.
Eriophorum vaginatum L.
E. angustifolium Roth.
Carex pulicaris L.
C. arenaria L.
C. echinata Murr.
C. ovalis Good.
C. nigra (L.) Reich.
C. flacca Schreb.
C. pilulifera L.
C. panicea L.
C. binervis Sm.
C. lepidocarpa Tausch.
C. tumidicarpa Anderss.
Anthoxanthum odoratum L.
Alopecurus geniculatus L.
Agrostis canina L.
A. stolonifera L.
A. tenuis L.
Ammophila arenaria (L.) Link.
Aira caryophyllea L.
A. praecox L.
Holcus lanatus L.
Arrhenatherum elatius Mert. & Koch.
Sieglingia decumbens Bernh.
**Phragmites communis* Trin.
Cynosurus cristatus L.
Molinia caerulea Moench.
Poa annua L.
P. pratensis L.
P. trivialis L.
Glyceria fluitans Br.
Puccinellia maritima (Huds.) Link.
Festuca ovina L.
F. vivipara Sm.
F. rubra L.
**Bromus mollis* L.
Lolium perenne L.
Agropyron repens Beauv.
A. junceum Beauv.
Nardus stricta L.
†*Pteridium aquilinum* Kuhn.
Blechnum Spicant With.
Athyrium Filix-foemina Roth.
†*Dryopteris Filix-mas* Schott.
†*Polypodium vulgare* L.
Equisetum arvense L.
**E. palustre* L.
**E. limosum* L.

STUDIES ON GONATORRHODIELLA HIGHLEI A. L. SMITH.

By W. BLYTH. (With Pls. IV–VII.)

(Read 19th May 1949.)

Gonatorrhodiella, a genus of the Fungi Imperfecti, is regarded as being composed of two valid species (Ayers, 1941) which are of interest not only because of their unique morphological characteristics, but also by reason of their comparative scarcity, curious geographical distribution and their association with other fungi in nature. The genus was originally created by Thaxter (1891) in order to accommodate a fungus which he discovered in Connecticut, and of which he stated:

"This species has been met with in several localities about New Haven always growing directly upon, or running a short distance from, certain species of *Hypocrea* and *Hypomyces* on which it appears to be parasitic."

Accordingly, he named the fungus *G. parasitica*, and Ayers (1941) considers the same species to have been collected by von Hoehnel, who observed the fungus growing on *Tremella lutescens* in Wiener Wald, and recorded it in 1907 as *G. eximia*. Davidson (1935) also mentioned the occurrence of *G. parasitica* in association with *Trichoderma lignorum* on a sporophore of *Polyporus* sp., and on *Betula nigra* decayed by a species of *Fomes*. Petch (1937) made the first British record when he found the fungus growing on *Hypomyces aurantius* at Totnes during the foray of the British Mycological Society in 1935.

The original description of the structure and occurrence of the other species of the genus, *G. Highlei* (Brown Mould), is the only one in which no other fungus is mentioned as an associate. The fungus was found growing on onion bulbs at Kew by Smith and Rea (1908) in 1907. All subsequent recordings of the species have been made in North America. The collections on which these reports are based are described by Ayers (1941) in a paper which deals with the persistent association of *G. Highlei* with *Nectria coccinea* (Pers.). The latter fungus, together with the scale insect *Cryptococcus fagi* Baer., is responsible for the bark disease of the beech, *Fagus grandifolia* Everhardt, in North America, and so constant is the occurrence of *G. Highlei* with the *Nectria* species that it is possible to detect beech-bark disease by the conspicuous clay-coloured patches to which the *Gonatorrhodiella* gives rise when in a freely sporing condition on the surface of the bark. It may therefore be regarded as an "indicator plant."

General accounts of the beech-bark disease have been given by Ehrlich (1934) and Spaulding (1948), and the *Nectria* species concerned is described by Lohman and Watson (1943) under the name *Nectria coccinea* var. *faginata* Lohman, Watson and Ayers. The beech scale, *Cryptococcus fagi*, commences the disease by infesting the surface of healthy beech bark in the form of colonies. The insects feed by means of stylets through which food materials are sucked from the plant tissues, and which are inserted as far as the phloem. The areas of bark which die as a result of feeding activities become sunken, and cracks form at the edges of the killed areas. Infection by the *Nectria* species is brought about by its entry through the bark cracks and the insect stylet tracks, and the subsequent death of the trees so infected is the outcome of the invasion of the cortex, phloem, cambium and sap-wood by *Nectria* hyphae.

Spaulding (1948) mentions the prevalence of *G. Highlei* in association with the *Nectria* sp. since 1929 in Nova Scotia and New Brunswick, and also includes references to various towns in the United States from which the fungus has been recorded. He states that: "Observations show it to be widely distributed in the colonies of the *Nectria* old enough to have developed abundant fruiting which seems to be necessary for this dependent fungus successfully to establish itself. It has been found only on *Nectria coccinea* var. *faginata* and is believed to be parasitic on it." The successional nature of the beech-bark disease is also emphasised in his paper, and he remarks that: "The association of an insect and two fungi in a serious disease of forest trees is believed to be unique in forest pathological literature."

Attempts have been made to grow both *G. parasitica* and *G. Highlei* on artificial substrates under laboratory conditions. Davidson (1935) found it impossible to culture *G. parasitica* in the absence of *Trichoderma lignorum* with which it occurred in its natural habitat, and concluded that a type of parasitism was involved. Ayers (1941) succeeded in growing *G. Highlei* in pure culture on an oatmeal mush and in the presence of *Nectria coccinea*, *N. galligena* and *N. cucurbitula*. Negative results were gained with *N. cinnabarina* and *N. coryli*.

Although both species of *Gonatorrhodiella* have been regarded and frequently referred to as parasites, no direct evidence of the relationships which they bear to their fungal associates has been put forward. The present paper is an attempt to resolve a part of this problem of fungal association in the light of the results of an investigation of *G. Highlei*, which was found at the Royal Botanic Garden, Edinburgh (Blyth, 1949), growing on the bark surfaces of a beech and a poplar log which had been stored in a wood pile for some months.

THE NATURAL OCCURRENCE OF THE FUNGUS.

In its natural surroundings the fungus is conspicuous. The globular, sporiferous heads of the conidiophores, which are given off from a basal mycelium in great profusion, are cinnamon buff to xanthine orange or clay (Ridgway, 1912) in colour in the mass, and patches of them form at the surface of the bark of the trees on which they occur (Pl. IV, fig. 1).

The distribution of the fungus on the two logs which were examined in Edinburgh differed appreciably. On the beech log the fungus was found to be growing directly upon, and conforming in extent with, the perithecial stromata of a colony of *Nectria cinnabarina* (Tode) Fr., a species of *Nectria* with which it has not been previously known to associate. The conidiophores of the *Gonatorrhodiella* formed patches some six inches square. The surrounding areas of the bark, which were free of *Nectria* stromata and were not colonised by the *Gonatorrhodiella*, supported fructifications of *Didymium nigripes*.

On the poplar log the conidiophores of the *Gonatorrhodiella* occurred exclusively in the cracks of the bark surface, forming an irregular pattern, and no other fungal fructifications were observable macroscopically.

I. OBSERVATIONS ON THE MORPHOLOGY AND CYTOLOGY OF THE FUNGUS.

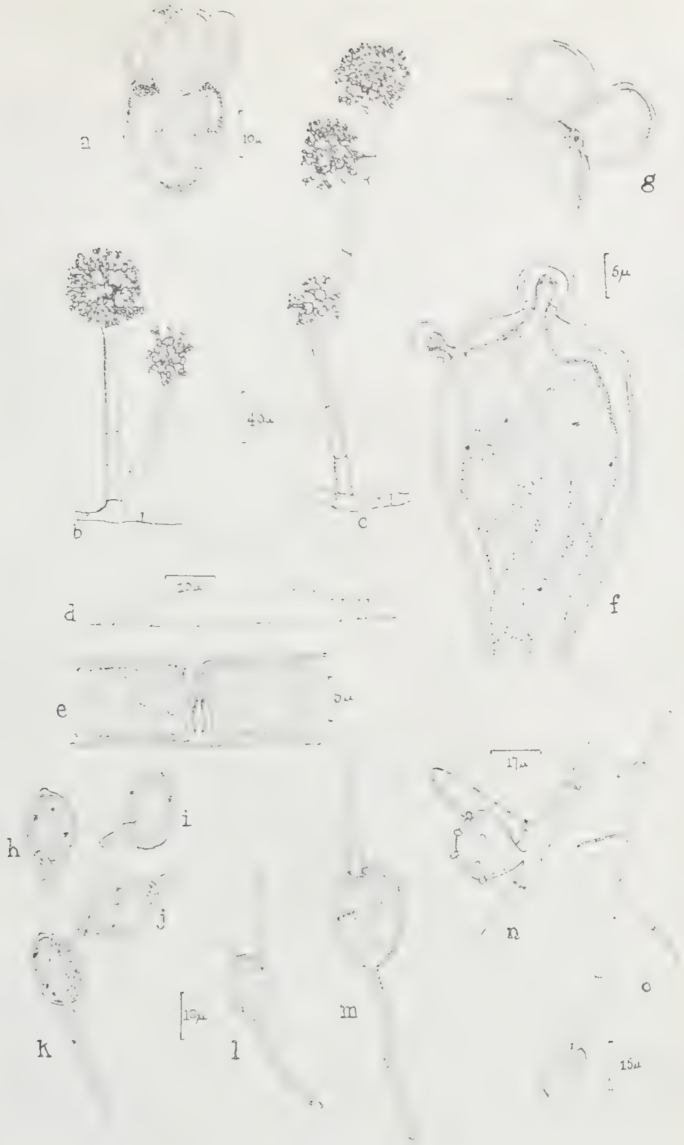
The vegetative mycelium of *G. Highlei* is composed of hyaline, septate, branched hyphae, 5–8 μ in width. The protoplasmic content of the hyphae is variable. Those cells nearest the growing tips contain abundant granular protoplasm, whilst those in the older parts of the mycelium become progressively more vacuolate in appearance and finally lose all functional contents. Irregularity in septation was also observed. Groups of two to five septa may be laid down at various points in the hyphae, so that cells 16–25 μ in length are frequently separated by short cells which may be 3–6 μ long (text-fig. 1, *d*).

Each conidiophore arises as a lateral protuberance from a cell of the mycelium. The protuberance increases steadily in length, becomes obtusely pointed, and is eventually cut off from the parent cell by a transverse septum. In most instances the width of the conidiophore initial varies from 8–10 μ, but occasionally conidiophore initials 5–6 μ wide have been observed. In conidiophores derived from the latter, dilation takes place a short distance from the parent cell, so that, when maturity is reached, the base of the conidiophore appears to be constricted.

By continued growth and development the initial cell gives rise to a simple cylindrical conidiophore, which is 10–15 μ in diameter and possesses a variable number of cells (3–7) before the production of conidia occurs. When the conidiophore has attained the height of 200–250 μ the terminal cell undergoes swelling at its distal end, becoming club-shaped. Terminal bulbs which are produced in this way may be elliptical or subspherical in shape when mature ($23 \times 42\ \mu$), and from their surfaces primary conidia or nodal cells are given off in a regular pattern.

The primary conidia are obovate in shape and may produce two to five secondary conidia from their distal ends. The primary conidia vary in length from 14–20 μ and at their widest points are 13–16 μ across (text-fig. 1, *a*). The secondary conidia agree in shape with the tertiary and quaternary conidia, which are later produced, in being elliptical. General measurements of the last three series of conidia are $13–15 \times 7–10\ \mu$. The arrangement of conidia given off from the conidiophore is therefore in chains, where the first branching of each chain is initiated from the primary conidia. Subsequent branching may also occur from the distal ends of the secondary and tertiary conidia, each of which may produce two conidia. The mature sporiferous head of the conidiophore assumes the form of a ball composed of closely approximated conidial chains (Pl. IV, figs. 2, 3 and 4).

Conidiophores display proliferation by which continued sporing is facilitated. The method involved incorporates further apical growth from the sporing terminal bulb. In most cases a single apical protuberance commences this growth, although two may be formed. By continued development of the outgrowth a short extension of the conidiophore is produced, which gives rise to a further sporiferous bulb, which in turn is capable of proliferation. In the material examined, proliferations rarely exceeded four in number. Text-fig. 1, *c*, shows an example of proliferation in which the original outgrowth from the first-formed sporiferous head has



TEXT-FIG. 1.—*Gonatorrhodiella Highlei.*

(*a*) Primary conidium bearing a terminal group of secondary conidia.
(*b* and *c*) Conidiophores.
(*d*) A part of the basal mycelium, showing irregularity of septation.
(*e*) Part of a mature conidiophore, showing the presence of a septal pore.
(*f*) Terminal bulb of a young conidiophore, showing the development of primary conidia.
(*g*) Early stages in the development of primary conidia from the terminal bulb of a young conidiophore.
(*h*, *i*, *k*, *l*) Germination of tertiary conidia.
(*j*) Germination of a secondary conidium.
(*m*) Germination of a primary conidium.
(*n*) Production of submerged conidia in old cultures.
(*o*) Development of the mycelium on fungal extract agars.

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introduced branching in the conidiophore. Branching is most commonly brought about in this way, but in rare instances has been observed to occur in the young conidiophore (text-fig. 1, *b*).

Owing to proliferation and branching, conidiophores may attain the height of 350–400 μ, and when fully mature are yellowish brown in colour by transmitted light. Coloration is due in part to the thick cell walls and in part to the protoplasm.

In order to examine the processes attendant on the formation of conidia and the general details of the structure of the fungus, conidiophores and mycelium were stained by the following method. The material was transferred to slide plates of plain agar, to which it adhered sufficiently to allow it to be passed through fixing and staining fluids. Fixation was carried out in alcohol-formalin-acetic (weak) for two hours, and successful staining accomplished by immersion in iron alum haematoxylin or basic fuchsin. Prior to examination, slides were mounted in lactophenol.

The cells of the mycelium and conidiophores of the fungus are multinucleate, the nuclei being dispersed in the cytoplasm, within which globular inclusions, presumably of a fatty nature, are also present. The conidia are also multinucleate, and all four series of conidia are produced from their parent structures in a similar way.

Each primary conidium arises as a sac-like outgrowth of the cell-wall of the terminal bulb of the conidiophore. As it increases in size it receives an inclusion of cytoplasm and nuclei from the conidiophore (text-fig. 1, *f*), and by the inward growth of the cell-wall at the point of origin of the young conidium, a transverse septum with a distinct central pore is laid down (text-fig. 1, *g*). The pore closes when the conidium is nearing maturity, so that the conidium is borne on a short sterigma. Secondary conidia arise from the primary, tertiary from the secondary, and quaternary from the tertiary by a similar process of development. In all types of conidia, which are released by the eventual fracture of sterigmata, the point of their attachment to the structures from which they were derived is shown by the presence of a hyaline papilla.

Both in the mycelium of the fungus and in the conidiophores the transverse septa commonly show a distinct septal pore. The pore is set in the centre of the septum in a thin zone of the cell-wall and may be easily seen in those hyphae which are partially plasmolysed. A fine thread of protoplasm passes through the pore to connect the protoplasts of adjacent cells (text-fig. 1, *e*).

II. Taxonomic Considerations.

The general morphology of the fungus is in agreement with that described for other representatives of the species by Smith (1908) and Ayers (1941). In his technical account of the fungus, Ayers states that: "The conidia . . . are elliptical and borne in complex trigeminous chains on obovate, nodal cells." The number of secondary conidia produced by the primaries (or nodal cells) varied in the specimens examined in Edinburgh from two to five. The most usual number recorded was four, and it is interesting to note that Smith (1908), in her original illustrations of the fungus, shows a primary conidium bearing four secondaries, presumably a condition representative of the fungus she examined. The European members of the species may, therefore, differ from the American with regard to this character.

The distinction between the two species of *Gonatorrhodiella* is based upon the nature of the primary conidia and the number of spore chains produced from them. In *G. parasitica* the primary conidia are elliptical and each gives rise to a single apical row of conidia, whilst in *G. Highlei* the primary conidia are obovate, bearing a variable number of conidial chains. From a study of the paper by Petch (1925) in which he describes and illustrates the entomogenous fungus "*Gonatorrhodiella coccorum*", the writer is in agreement with Ayers (1941) in excluding this fungus from the genus *Gonatorrhodiella*, with which it shows little morphological affinity.

In his original description of the genus, Thaxter (1891) considered it to be mucedinous, and commented on the resemblance which it bore to *Gonatorrhodum* (Corda), regarded by Saccardo as a member of the Dematieae. The genus is grouped by Engler and Prantl (1900) in the Gonatobotrytideae of the Mucedinaceae-Hyalosporae. The three genera, *Gonatobotrys* (Corda), *Nematogonium* (Desm.) and *Gonatorrhodiella* (Thaxt.), which are placed in the Gonatobotrytideae, agree in possessing a conidiophore showing intercalary fertile cells bearing conidia. In the first two named genera, however, conidia are produced singly, the presence of conidial chains serving to distinguish *Gonatorrhodiella*.

It is suggested that features in the morphology of *G. Highlei* are analogous to those found in *Botrytis angularis* A. L. Sm. This fungus, described and illustrated by Smith (1898), shows the development of terminal, angular, bladder-like cells of the conidiophore, which bear obovate, swollen cells similar in appearance to the primary conidia of *G. Highlei.* These swollen cells produce groups of elliptical conidia borne on sterigmata. The resemblance is further substantiated by the fact that the conidiophore of *B. angularis* may continue its growth and form other sporiferous heads at a higher level. The tendency to produce a conidiophore in which inflated fertile cells assume an intercalary position suggests affinity with the Gonatobotrytideae. *B. angularis* appears to assume a position intermediate between such forms as *B. cinerea* and *B. Preussii* in the Botrytideae and *G. Highlei* in the Gonatobotrytideae.

III. The Relationship between Gonatorrhodiella Highlei and other Fungi in Nature.

In order to study the relationship between *G. Highlei* and other fungi in nature, a general investigation of the areas of the beech and poplar bark, which showed freely sporing colonies of the fungus, was undertaken.

The fungus on the beech bark was examined by cutting hand sections through the perithecial stromata of *Nectria cinnabarina*, above which a rich growth of conidiophores was to be found. The sections showed that the basal mycelium of the *Gonatorrhodiella* occurred principally in pockets, variably situated between the stroma proper and the erumpent *Nectria* perithecia, and also at the base of the stroma, sometimes encroaching into the pseudoparenchyma (Pl. V, fig. 5). From these localised areas of concentration of the mycelium, ramifying hyphae entered partly into the outer tissues of the bark, and also passed upwards to form loose patches of aerial mycelium lying between the *Nectria* perithecia. From the hyaline to cinnamon-buff patches of mycelium, stolon-like hyphae, bearing conidiophores at intervals along their lengths, were freely given off. The precise relationship between the pseudoparenchyma of the *Nectria* stromata and the basal mycelium of the *Gonatorrhodiella* could not be discovered from an examination of the sections. The close connection between the two fungi in a mechanical sense was, however, implied by the observation of the ramification of the hyphae of the *Gonatorrhodiella* mycelium within the pseudoparenchyma of the *Nectria* stromata in a number of cases. The hyphae could easily be distinguished in unstained preparations owing to their light coloration, which contrasted with the deeper brownish pigmentation of the cells of the stroma tissue.

An examination of the *Gonatorrhodiella* colony on the poplar log showed that the conidiophores, which arose from a basal mycelium situated in the cracks of the bark, were loosely invested by other fungal hyphae (Pl. V, fig. 6). The latter pursued a longitudinal growth. Arising from the substratum, where they freely intermingled with the hyphae of the basal mycelium of the *Gonatorrhodiella*, they ran in close contact with the conidiophores, the terminal bulbs of which were frequently encased by hyphal branches. The presence of such hyphae did not appear to have any detrimental effects on the sporing capacity of the conidiophores, the cells of which were normal in their development. In preparations mounted in water, slight pressure of the cover-glass served to dislodge investing hyphae, showing that the connection between them and the conidiophores was limited to a surface attachment.

IV. Studies on the Fungus in Mixed Culture.

An investigation of the fungus flora of the areas of poplar and beech bark, supporting colonies of *G. Highlei*, was carried out with particular reference to the poplar sample.

It has already been stated that the basal, loose plectenchyme from which the conidiophores arose on poplar bark contained a variety of hyphae which belonged to other fungi, and that in many instances the conidiophores were invested in such hyphal growths. The fungi were therefore brought into culture by two methods. By the first of these it was hoped to establish the identity of the hyphae which invested the conidiophores. Mature conidiophores were removed aseptically from their situation at the surfaces of the bark by means of sharp-pointed forceps sterilised by flaming. The conidiophores were then either transferred directly to agar plates, or first shaken in sterile water and the resulting suspension of conidia and hyphal fragments plated out. The plates were poured in Petri dishes or on slides (Noble, 1937). The media used at this stage of the investigation were potato-dextrose, malt and plain 2·5 per cent. agars, and cultures were incubated at 18°–20° C.

The colonies which resulted from these isolations proved to be of a fungus provisionally identified as a species of *Nectria*, and in rare cases *Trichoderma lignorum* (Tode) Harz. was also obtained.

By the second method of isolation the basal mycelium of the fungus was subjected to the technique described above in order to obtain a general picture of the total fungus flora at the seat of origin of the conidiophores. From the plates which were obtained the dominant fungus was found to be the *Nectria* sp. with *Trichothecium* *roseum* Link subdominant. A small number of *Trichoderma lignorum* colonies were also recorded.

Similar investigations carried out with the beech-bark sample showed that the dominant fungus was *Nectria cinnabarina* (Tode) Fries., and that *Trichoderma lignorum* and *Trichothecium roseum* were also present.

Several plates, each inoculated with a number of conidiophores aseptically removed from poplar bark, and which yielded colonies of the *Nectria* sp., were kept for three months in the hope of recovering the *Gonatorrhodiella*. No aerial growth of the mycelium of the latter fungus could be discerned. From the plates examined microscopically, however, four in which the medium employed was potato-dextrose agar showed the presence of the larger hyphae of the *Gonatorrhodiella* interwoven with the finer *Nectria* hyphae at the surface of the agar. In several cases there was evidence of the degeneration of the *Gonatorrhodiella* hyphae. Many breakages were observed at the transverse septa, accompanied by extreme vacuolisation of the cell contents, indicating parasitism by the *Nectria* sp. No growth of the *Gonatorrhodiella* was ever observed in malt or plain agar cultures, and similar results were obtained when the fungus was plated in the presence of *Nectria cinnabarina*.

The transference of mature conidiophores from poplar bark to oatmeal mush, a medium reported by Ayers (1941) as suitable for promoting the growth of *G. Highlei*, gave freely sporing colonies of the *Nectria* sp. which filled the Petri dish within fourteen days of inoculation. The appearance of the *Gonatorrhodiella* in such colonies derived from mixed inoculum was retarded, and, under the conditions of incubation imposed, the production of aerial hyphae by the fungus rarely occurred before one month. The *Nectria* sp. gives rise to a colony which is loose and cottony in appearance and white in colour during early stages of growth. The white coloration gives way eventually to shades of yellow and then brown. As the *Gonatorrhodiella* develops, the hyaline aerial hyphae to which it gives rise form a sparse, loose network within the surface layers of the *Nectria* colony. The conidiophores are produced from these hyphae and appear in scattered groups, which are at first cinnamon buff to xanthine orange in colour. The groups coalesce, and the colony assumes a conspicuous clay or rufous pigmentation owing to the massed conidiophores. During this development the *Nectria* colony continues to spore without detriment. Microconidial fructifications, which develop within two to five days' growth, are eventually mingled with white to cream macroconidial sporodochia, which are clearly visible at various points amongst the conidiophores of the *Gonatorrhodiella.*

Technical Description of the Nectria Species.

Mycelium at first white, soon turning to shades of buff yellow, and felting down to become sayal brown and finally chestnut with age. Microconidia borne on the aerial mycelium in false heads on simple or branched conidiophores, mostly unicellular, occasionally 1-septate, hyaline, elongate-ovate. 0-septate $4{\cdot}2\text{–}8{\cdot}7 \times 2{\cdot}1\text{–}3{\cdot}6\ \mu$. Macroconidia borne on white or cream sporodochia, and in older cultures in columns 1–5 mm. in height, which become split and recurved with age, hyaline, 3–5 septate, elongate subcylindric, unequal-sided with obtusely rounded ends.

3-septate: $30\text{–}46 \times 5{\cdot}9\text{–}6{\cdot}4\ \mu$.
4-septate: $50\text{–}66 \times 6{\cdot}3\text{–}7{\cdot}0\ \mu$.
5-septate (rare): $62\text{–}74 \times 6{\cdot}6\text{–}7{\cdot}2\ \mu$.
Perithecia not observed in culture.

Owing to the absence of perithecia, the fungus cannot be fully identified. In the possession of a *Cylindrocarpon* macroconidial stage, which is of a columnar form, in the general type of growth of the mycelium, and in the coloration described above for cultures grown on potato-dextrose agar, the fungus resembles varieties of *Nectria coccinea* Pers., described by Lohman and Watson (1943).

Oatmeal mush was used throughout the investigation for the maintenance of sufficient quantities of *G. Highlei*, but the disadvantage of such substrates lies in their opacity, which constitutes a barrier to direct microscopic vision of fungi *in situ.* To study the relationship between the *Gonatorrhodiella* and the *Nectria* sp. in culture, experiments were conducted with a view to finding a medium which combined the property of transparency with the ability to supply the substances necessary for the germination of the conidia of the *Gonatorrhodiella* and the subsequent full development of mycelium and conidiophores. The medium which fulfilled these requirements was produced by boiling a one-month-old culture of the *Nectria* sp. or *Nectria cinnaborina* with ten grammes of beech bark for ten minutes in 100 c.c. distilled water. The filtrate from the decoction was then made up to 250 cc. with distilled water and agar incorporated to make a 2·5 per cent. medium.

Culture media of this type were also made up from one-month-old cultures of *Trichothecium roseum* and *Trichoderma lignorum*. These media were also found to be effective in promoting conidial germination of the fungus. All fungi grown on extract agars were found to maintain a regular growth at the surface of the media, although the development of aerial mycelium was small.

V. Conidial Germination in G. Highlei.

Conidial suspensions were made up by shaking conidiophores of the fungus, obtained from mixed stock cultures grown on oatmeal mush, in sterile water. The suspensions were plated on *Nectria*, *Trichothecium* and *Trichoderma* extract agars on slides which were incubated in darkness at 18°–20° C. Slides were removed from the incubator at daily intervals during a period of a fortnight, and, after a preliminary examination, were fixed in alcohol-formalin-acetic, prior to staining in iron alum haematoxylin or basic fuchsin.

Germination of the conidia of the *Gonatorrhodiella* occurred within four to five days, the proportion of germinations being greatest on the *Nectria* extract agar. Young colonies of the *Nectria* species, which had developed from conidia introduced with the spore suspensions, were also observable at this time.

Primary, secondary, tertiary and quaternary conidia of the *Gonatorrhodiella* were all observed to germinate. The primary conidia were easily distinguishable owing to their characteristic obovate shape, but the other conidia were determined on a basis of measurement. Germ tubes, which are hyaline or tinged with a faint yellowish coloration in unstained preparations, are usually produced singly from each conidium. The place of their origin may be proximal, distal or lateral. In cases where two germ tubes occur they are diametrically opposite.

The germ tube makes its first appearance as a rounded sac which becomes swollen at the upper end (text-fig. 1, *h*). Growth then proceeds from the apex of the sac, giving rise to a hypha which is filled with densely granular cytoplasm containing several nuclei. The hypha varies in width from 1·5 to 2·5 μ.

The shape of the original sac is retained in most cases as a slightly dilated zone a short distance from the point of origin of the germ tube (text-fig. 1, *i*, *j*, *k* and *m*). An abnormal case of germination in a tertiary conidium is given in text-fig. 1, *l*. Prior to the transfer to agar, the conidium had already given rise to the initials of two quaternary conidia at its distal end. Apart from the production of a germ tube at the proximal end of the tertiary conidium, a germ tube has also been formed from a quaternary conidial initial.

As growth of the germ tube proceeds, the protoplasmic content becomes vacuolate, and septa, which are difficult to distinguish during their early development, are laid down.

VI. THE RELATIONSHIP BETWEEN G. HIGHLEI AND THE NECTRIA SP. IN CULTURE.

Plates of the three types of fungal extract agars were flooded with mixed conidial suspensions of *G. Highlei* and the *Nectria* sp. The rapid growth of the *Nectria*, which follows germination of the conidia, causes the appearance of small fungal colonies bearing microconidial fructifications of the *Cephalosporium* type before the germ tubes of the *Gonatorrhodiella* are much greater than 300 μ in length.

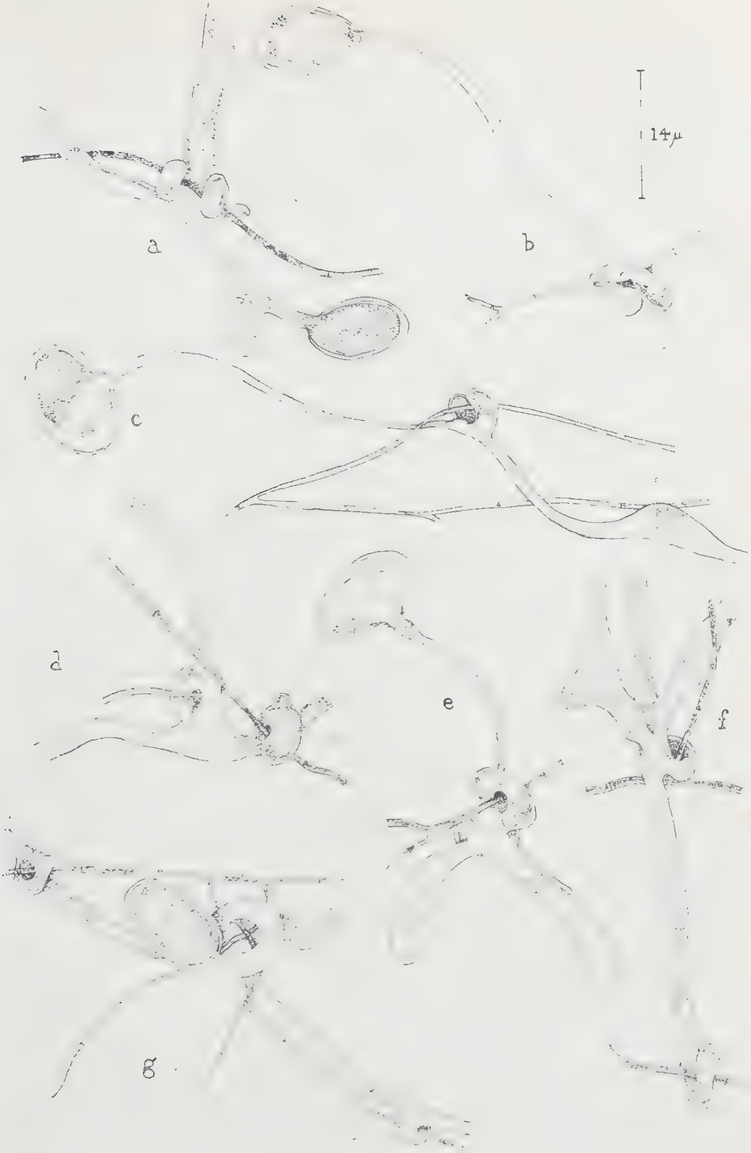
The development of the fungus in the presence of the colonies of the *Nectria* sp. may be considered to fall into three principal stages. Of these, the first is the formation of an appressorium by the germ tube when direct contact is made with the hypha of a developing *Nectria* colony and the later growth of the tip of the germ tube to form a hook which encircles the *Nectria* hypha. A further series of hooks may then arise from the appressorium.

The second stage, which follows directly upon the first, involves the formation of a prolific branch system of distended hyphae which has its origin in the appressorium and hooks.

The third stage comprises the growth and development of the branch system, which gives rise to a sparse ramifying mycelium, the hyphae of which form secondary appressoria and hooks on other hyphae of the parasitised *Nectria* colony. Conidiophores of the *Gonatorrhodiella* are developed either from the first formed branch system, or later from the hyphae of the mycelium.

As considerable variation occurs in the three stages of development, each stage will be described in detail.

(i) *The Formation of Appressoria and Hook Cells.*—At the point of contact with a *Nectria* hypha, the germ tube of the *Gonatorrhodiella* becomes dilated immediately behind the growing tip, and the dilation adheres closely to the host hypha in the form of an appressorium. The hyphal tip then continues its growth, finally assuming the form of a hook, which rings the *Nectria* hypha (Pl. V, fig. 7). The onset of the process appears likely to be conditioned by the amount of food reserve which the conidium releases to the developing germ tube. The formation of an appressorium and hooks is not necessarily undertaken at the first *Nectria* hypha



TEXT-FIG. 2.—Parasitism of the *Nectria* sp. by *G. Highlei*.

(*a, b, c and e*) Formation of appressoria (*x*) and hook cells (*z*) by the germ tube of *G. Highlei* when contact is made with the hypha of the *Nectria* sp.
(*d, f and g*) Development of secondary appressoria and hook cells by the branch hyphal system of *G. Highlei*.

which occurs in the path of growth, even though a near contact is operative, and in many instances the second hypha of the *Nectria* colony is parasitised. The width of the germ tube has been observed to become increased a short time after the formation of appressoria and hooks, the enlargement proceeding backwards towards the spore.

In the earliest stages of development the appressorium and hook are both products of the terminal cell of the germ tube. Eventually, however, the hook usually becomes cut off from the appressorium by the formation of a transverse septum situated at its base. Subsidiary hook cells may then arise from the dilation so that the host hypha is encircled at several closely approximated points (Pl. VII, fig. 11). An early stage in the development of multiple hook formation is shown in text-fig. 2, *a*, where two hook cells clasp the parasitised *Nectria* hypha.

The degree to which the original appressorium develops is variable. In many cases no appreciable dilation of the germ tube at the point of contact with a *Nectria* hypha may be observed. The tip of the germ tube normally gives rise to a hook cell, which ceases to grow further when the *Nectria* hypha, with which it is in contact, is only half encircled. A similar hook cell then arises from the zone of the germ tube at the base of the original hook, so that the host hypha becomes clasped between a pair of pincer-like hooks (text-fig. 2, *b* and *c*). Paired hook cells have also been observed to arise laterally from a cell of the germ tube (Pl. VI, fig. 10).

Irrespective of their origin, it is clear the hook cells are to be regarded as special structures, effecting the removal of substances from the host. They show no further growth in length, and in many cases undergo no further development of any kind. The repeated examination of stained preparations has failed to reveal the occurrence of direct penetrations of *Nectria* hyphae, either by appressoria or hook cells. That the connection between the two fungi is a close one is nevertheless borne out by the fact that it has not been possible to separate them, even by the use of needles. There is also some evidence to show that the free ends of the hook cells may become fused with the appressorium from which they are given off at a later date, and may thus form closed rings about the *Nectria* hyphae.

Over a period of some six weeks no change is visible in the parasitised *Nectria* hyphae, which continue to give rise to microconidia in great profusion. In cultures eight to ten weeks old, however, several parasitised hyphae have been observed to show constriction at the zone to which the hook cells of the germ tube are attached. No vacuolisation or other manifestations of degeneracy were involved.

(ii) *The Formation of the Branch System.*—The stimulus for prolific branching, which precedes the development of the mycelium of the fungus, appears to be provided only by the parasitism of a *Nectria* hypha.

The appressorium produced by the germ tube undergoes increase in size within twelve hours of its first production of a hook cell or series of hook cells. Septation does not occur, and the appressorium is filled with a granular mass of protoplasm which is richly provided with vacuoles. From an examination of stained preparations, it has been found to be multinucleate, the nuclei being dispersed within the cytoplasm. After a further twelve to twenty-four hours' incubation at 18°–20° C. the initials of branch hyphae arise from the periphery of the appressorium.

Branch hyphae may be two to five in number, and from their first development are 5–6 μ in diameter. As the growth of the hyphae proceeds, they become septate and vacuolate (Pl. VI, figs. 8, 9, 10; Pl. VII, figs. 11, 12; text-fig. 2, *e* and *g*).

In those instances where no dilation of the germ tube precedes the development of hook cells, the branch system arises as hyphal initials from the lateral cell-walls of the hooks (text-fig. 2, *b*).

(iii) *The Development of the Mycelium.*—The branch hyphae enter a phase of rapid growth. Side branching is rare for several days, and further hook cells are formed when contact is made with other hyphae of the *Nectria* colony. Hook cells arise either as lateral outgrowths from hyphal cells which may or may not become previously distended, or develop, as did the first hook cells of the germ tubes earlier described, from the growing hyphal tip. Examples of secondary hook cells are shown in Pl. VI, fig. 9, text-fig. 2, *g*, *d*, *f*, and an early stage in the development of a lateral appressorium is shown in text-fig. 2, *c*. These secondary hook cells also give rise to lateral branches, although their own growth in length is curtailed after the host hypha has been encircled.

In cultures which have been incubated for about a month some hyphae of the *Gonatorrhodiella* colony become free at the surface of the agar, to form a loose network within the upper zones of the surrounding *Nectria* mycelium. Hook cells are rarely developed by these aerial hyphae when the fungus is grown on fungal extract agars, but have been observed on rare occasions in cultures grown on oatmeal mush. It appears, therefore, that the occurrence of appressoria in culture is principally confined to the surface or subsurface areas of the substratum, and that the aerial hyphae derive sufficient food products from these contacts to remain independent of the hyphae which constitute the aerial mycelium of the *Nectria* colony.

(iv) *The Development of Conidiophores and Variations in their Morphology.*—Conidiophores may arise from the branch hyphal system which follows the formation of the first appressorium by the germ tube. Each conidiophore is the product of the lateral extension of a hyphal cell, and the terminal sporiferous bulb frequently develops when the conidiophore is only two or three cells in length. On fungal extract agars the conidiophore may be 50–150 μ in length before the production of conidia occurs (Pl. VII, figs. 11 and 12).

The development of the fungus from the germination of the conidium to the production of a young conidiophore is shown in Pl. VII, fig. 11. In this case the *Nectria* hypha shows encirclement by three hook cells, and the conidiophore arises directly from an immediate hyphal branch of the prolific growth system which has been the outcome of parasitism.

Variation in the development of the conidiophores particularly affects the degree to which the terminal bulb is developed, and the number and arrangement of the primary conidia. In the most extreme cases the terminal bulb is scarcely delimited from the remainder of the conidiophore, and bears a single apical primary conidium (Pl. VII, fig. 12). In more normal conidiophores, the primary conidia are grouped around the bulb in a symmetrical arrangement (Pl. VII, fig. 11). It is worthy of mention that the obovate shape of the primary conidia, an important specific character of the fungus, remains constant, and they are always larger than the secondary and tertiary conidia which follow.

Extreme variation, concomitant with the production of submerged conidia, has been observed twice in culture. An example is shown in text-fig. 1, *n*, where a lateral hypha of the ramifying subsurface mycelium has become swollen into a bulbous structure bearing small, hyaline, ovate conidia, 2×3 μ in size, irregularly at the upper end. These structures are considered anomalous, as they appeared in four-month-old cultures. Observations suggest that they play no significant part in the normal life-history of the fungus, either in culture or in nature.

VII. Studies on the Fungus in Pure Culture.

The fungus was brought into pure culture by removing conidia and hyphal fragments from slide cultures, on which mixed suspensions of *Nectria* and *Gonatorrhodiella* had been poured, to fresh plates. Removal was effected by means of a dummy objective, and transferences were made to oatmeal mush, and to potato-dextrose, malt, plain and fungal extract agars.

The conidia were found to germinate readily on fungal extract agars, germination being identical with that already described from observations made on mixed cultures. The growth of the germ tube, which remained 1·5–2·5 μ in diameter, was extremely slow, and ceased after a period of two months. During growth, branches derived from lateral extensions of a few cells of the original germ tube were produced at an obtuse angle to the axis of the germ tube and appeared reflexed. An example of a colony of the fungus after two months' growth is shown in text-fig. 1, *o*. Limited growth of hyphal fragments was also achieved on fungal extract agars.

Neither conidial germination nor hyphal regeneration was recorded on malt, potato-dextrose or plain agars, and conidia pre-germinated on fungal extract agars showed no further growth. Oatmeal mush gave a certain growth of mycelium after planting with pre-germinated conidia. Hyphal growth was sparse, the colony assuming a white colour, and growth ceased after a month and before the production of conidiophores.

Discussion.

That *Gonatorrhodiella Highlei* is definitely a parasite has been shown by observations made on its behaviour in culture. When in pure culture, the growth of the fungus which follows germination of the conidia is poor, and the lateral branches of the hyphae are produced at an obtuse angle. The behaviour of the fungus in the presence of the *Nectria* species presents a marked contrast. On fungal extract agars, prolific growth of the fungus is initiated only after the germ tube has made contact with a living *Nectria* hypha.

In his experimental work with *G. Highlei* Ayers (1941) succeeded in bringing the fungus into pure culture on synthetic malt, potato, potato-dextrose, and malt agars, a scanty mycelial growth occurring on all media, and the development of conidiophores only on synthetic malt. On oatmeal mush he obtained freely sporing, vigorous cultures. In the present work, oatmeal mush and fungal extract agars were the only media which gave any mycelial development in

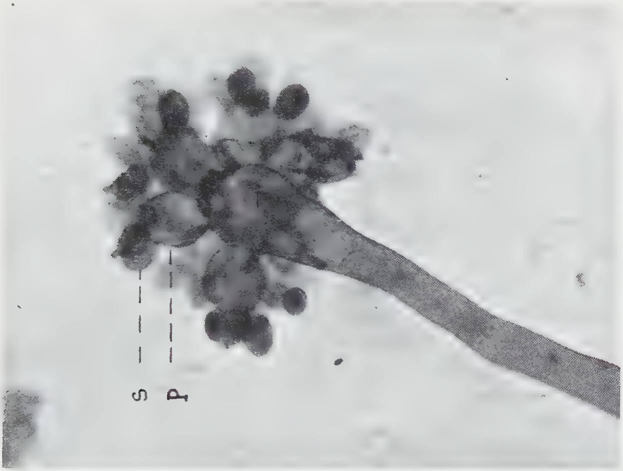


Fig. 2.

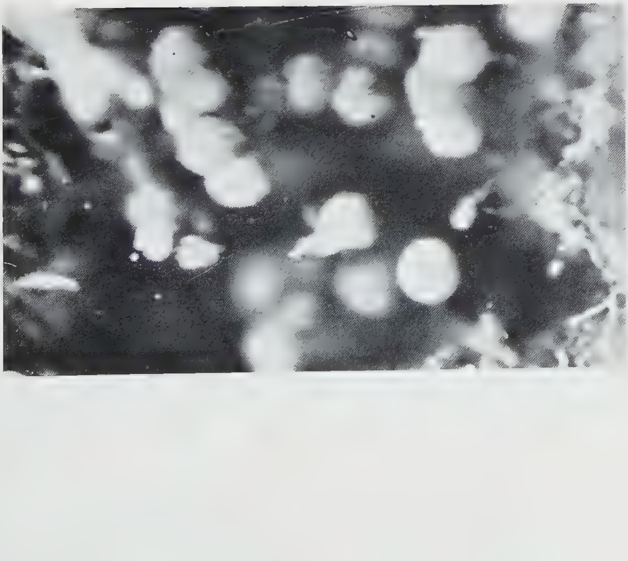


Fig. 1.

W. Blyth.

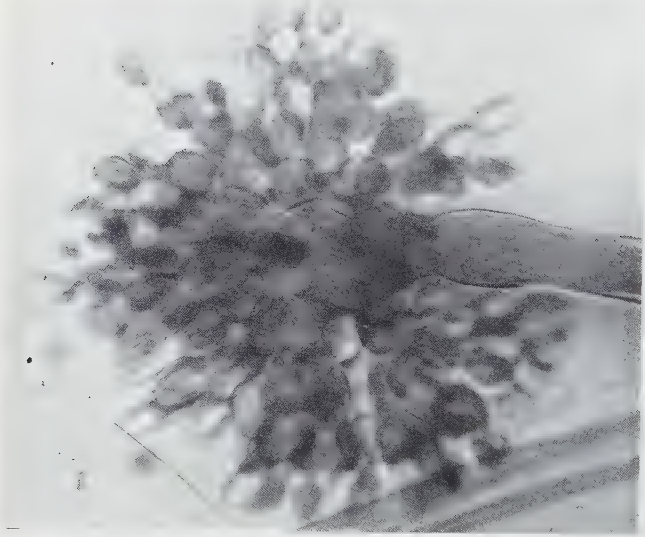


Fig. 4.

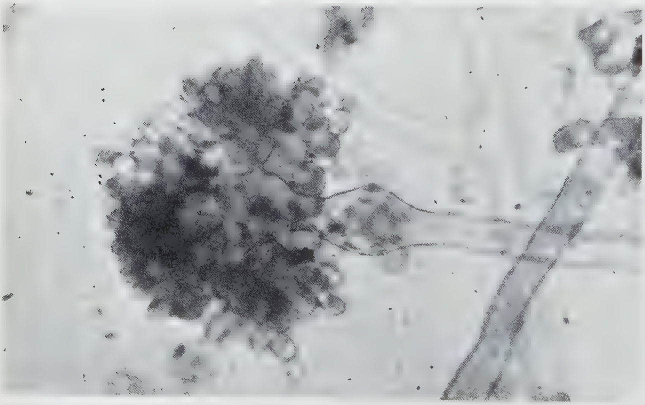


Fig. 3.

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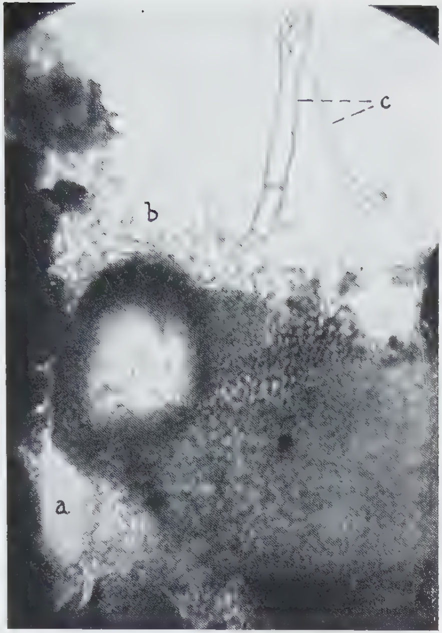

FIG. 5.

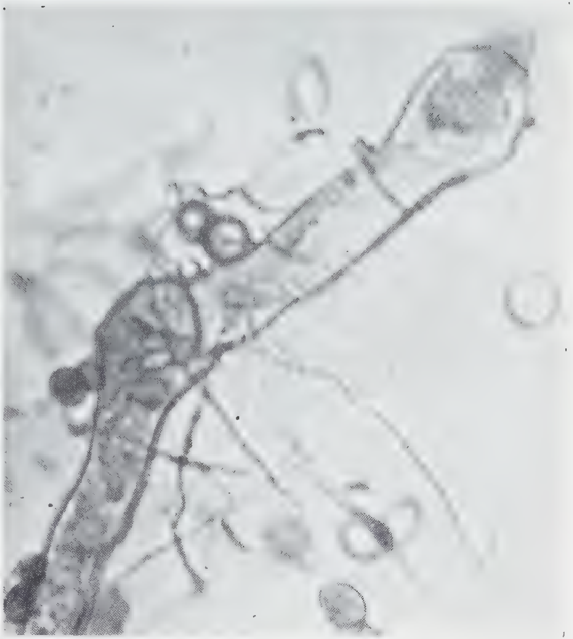

FIG. 6.

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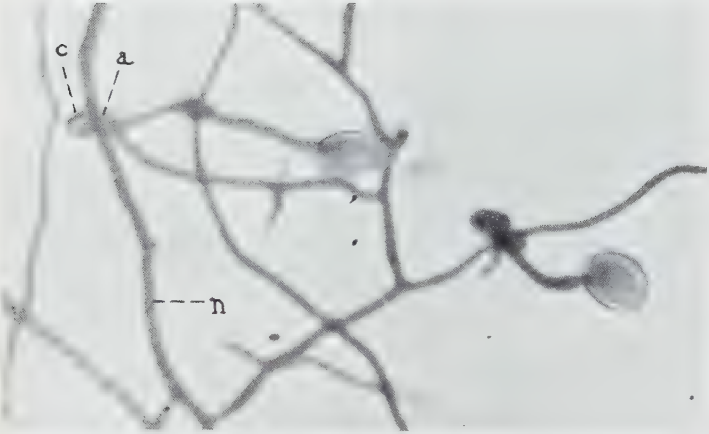

FIG. 7.

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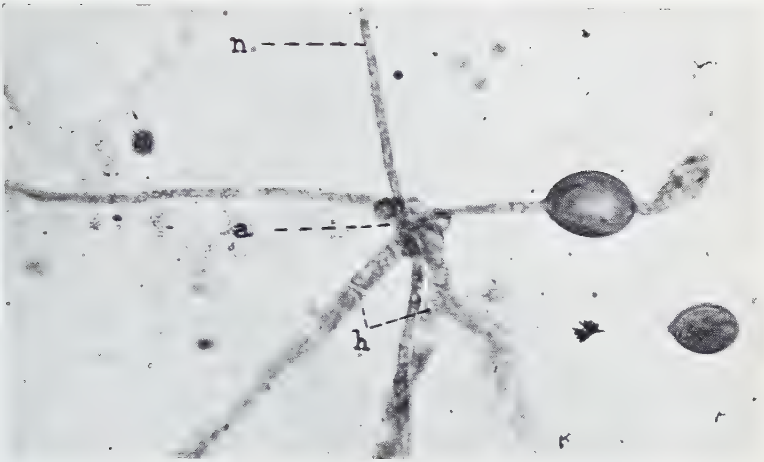

Fig. 8.

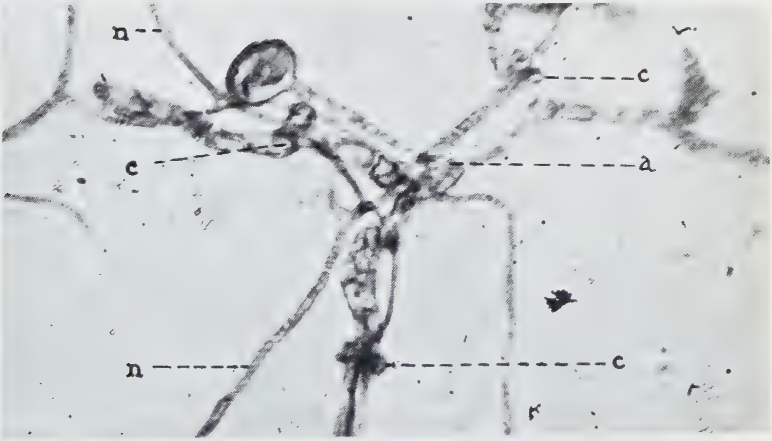

Fig. 9.

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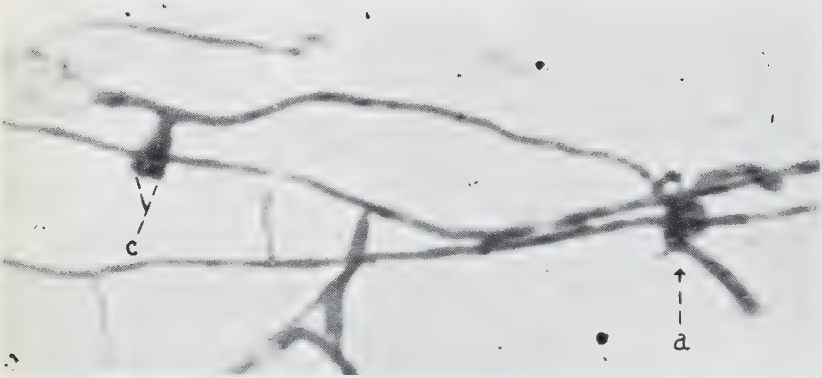

Fig. 10.

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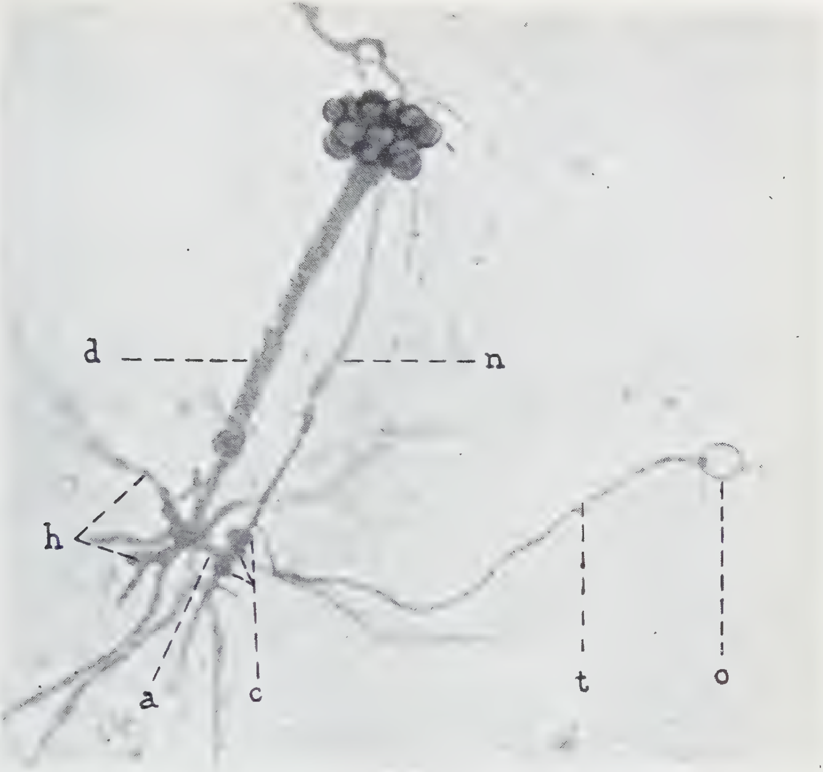

FIG. 11.

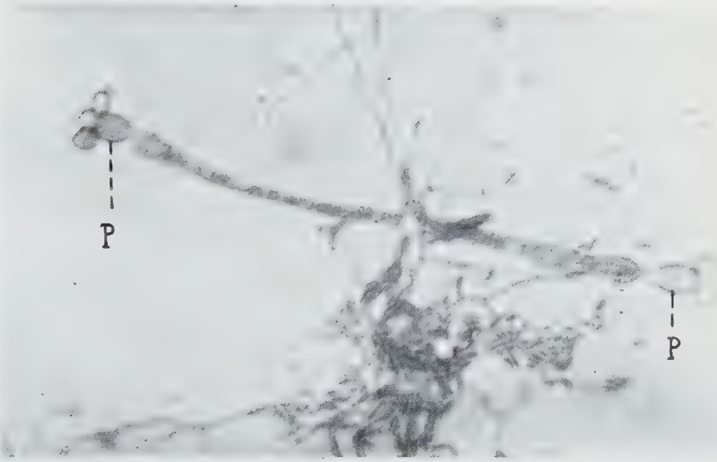

FIG. 12.

W. BLYTH.

pure culture, and conidiophores were never observed. In mixed culture, parasitism was found to be reversible on potato-dextrose agar and could not be obtained on malt and plain agars, although it was easily established on oatmeal mush.

It seems, therefore, that the capacities of *Gonatorrhodiella* isolates for the development of parasitism on agar media may vary, as it is apparent that the *Gonatorrhodiella* cultured in Edinburgh more nearly approaches the obligate state than the North American isolates of the fungus described by Ayers. The relationship between *G. Highlei* and the species of *Nectria* is suggested as one which is dependent on the substratum, in that changes in the nutrient component of the substratum may inhibit or reverse parasitic activity. The difficulty of growing *G. Highlei* on agar substrates was particularly stressed by Ayers, who cited several parallel cases of fungi parasitic on insects and on other fungi. It is not clear, however, whether the difficulty of culture is to be considered purely as the outcome of the inclusion of agar in the medium, or as due to the absence of various biochemical substances.

Regarding the germination of conidia, Ayers stated: "To secure pure cultures of *Gonatorrhodiella Highlei*, single spore isolations were used at first. However, these conidia failed to germinate on the different media used, and even to date the conditions necessary for their germination have not been discovered." It has been shown in the present work that extracts prepared from *Nectria cinnabarina*, a second *Nectria* sp., *Trichothecium roseum* and *Trichoderma lignorum*, which were growing in close proximity to the *Gonatorrhodiella* in nature, would, when incorporated singly into agar media, provide substances which were capable of stimulating both conidial germination and a limited hyphal growth of the *Gonatorrhodiella*. Although it has not been within the scope of the investigation to define the nature of the substances promoting conidial germination, it is of interest that they are heat-stable, and it seems likely that they are easily diffusible growth products. The results obtained with *Trichothecium roseum* and *Trichoderma lignorum* are in some ways paradoxical in view of the antifungal properties of their extracts reported by Freeman and Morrison (1948) and Weindling (1934, 1936, 1937) respectively.

The behaviour of *G. Highlei* under natural conditions may well be governed by the diffusion of substances from surrounding fungi, the point of greatest interest being that the substances do not appear to be necessarily produced only by the fungal host of the *Gonatorrhodiella*. The investigation has served to show that fruiting of the

Nectria sp. is not a prerequisite of the development of the parasite, as is suggested by Spaulding (1948), quoted in the introductory section of the present paper, but that parasitism may be established both in the laboratory and in the field on mycelia possessing, at most, only asexual reproductive stages.

The association between *G. Highlei* and *Nectria cinnabarina* is one which has not been previously recorded. The parasitism in culture of *N. cinnabarina* by the *Gonatorrhodiella*, which was found in association with the other *Nectria* sp. on poplar bark, could not be brought about on any media, but the natural association is to be upheld by virtue of the close connection between the pseudoparenchyma of the *Nectria* stroma and the *Gonatorrhodiella* mycelium, and by the absence of any other *Nectria* species within the bark of the beech log which could have represented an associate.

The comparatively few papers which have dealt with the parasitism of one fungus on another describe types of parasitism which vary both in the mechanism adopted by the parasite and in the effect which is produced in the host. It is therefore proposed to describe examples of these types of parasitism and to discuss the parasitism of *G. Highlei* in the light of the generalisations which may be drawn from them.

Parasites which effect a complete and relatively rapid degeneration of their hosts frequently adopt an eventual penetration of their host cells, and may actively produce toxic substances by which degeneration is instigated and accelerated. A fungal association incorporating these principles was reported by Weindling (1932), who gave an account of the parasitism of *Rhizoctonia solani*, *Sclerotium rolfsii* and species of *Pythium*, *Phytophthora* and *Rhizopus* by *Trichoderma lignorum*. In these associations, parasitic activity is developed by the lateral hyphae of the *Trichoderma*, which coil tightly round the host hyphae, the protoplasm of which undergoes coagulation and loss of vacuolar structure. The host hyphae also suffer breakages at the transverse cell septa, and bursting in those instances where the hyphae of the parasite and host approach under submerged conditions in culture. The active toxic principle elaborated by the hyphae of the *Trichoderma* was later made the subject for researches (Weindling, 1934, 1936, 1937).

Warren (1948) records a similar form of parasitism of *Rhizoctonia solani* by *Papulospora stoveri*, the lateral hyphae of which form coils about the hyphae of the host. The protoplasm of the host hyphae becomes separated into two parts at the point where a lateral branch of *Papulospora* develops, and a general degeneration sets in.

Direct penetration of the host is a feature of *Trichoderma* and *Papulospora*, unmodified hyphae entering moribund parts of the host. The external method of attack is, however, more prevalent than the internal.

Reinhardt (1892) has provided instances of host degeneration which is brought about by the parasitic activity of *Peziza* (*Sclerotinia*) species, in which no internal penetration is operative. The "*Peziza*" species described showed active parasitism towards *Mucor mucedo*, *M. racemosus*, *Rhizopus nigricans*, *Phycomyces nitens*, *Dematium* (*Pullularia*) *pullulans*, *Acrostalagmus cinnabarinus*, *Trichothecium roseum* and *Fumago salicina*. On *Phycomyces*, *Rhizopus* and the *Mucor* species, the lateral hyphae of the "*Peziza*" either form coils about the host hyphae, finally forming a dense felt, or are more limited in growth, developing a tuft of short, peg-like branches when contact is established with the hyphal wall of the host. The vegetative hyphae of the host are eventually destroyed, and ascending fertile hyphae suffer a similar disintegration.

In the above examples no complete differentiation of specialised hyphal organs has been in evidence. The parasites concerned are all organisms which attain the destruction of their hosts by means of lateral hyphal branches, which show little evidence of modification. When penetration does occur, the penetrant hyphae are morphologically similar to the remaining hyphae of the mycelium.

Parasitism which is effected through the agency of specialised haustorial organs is seen in *Dispira cornuta* when parasitic on *Sporodinia grandis* (Ayers, 1935). In this fungus the germ tube which is produced on germination of the conidium becomes septate and branched, and some of the branches parasitise the vegetative hyphae of the host. The appressoria which are developed assume a knob-like appearance, and give rise to slender penetration tubes which enter the host hyphae, and then develop finger-like haustorial branches. Haustorial development has been shown to exist in *Syncephalis* (van Tieghem, 1875) and *Piptocephalis* (Brefeld, 1872), and morphologically and functionally emulates that in *Dispira*. Under aquatic conditions, *Rhizidiomyces apophysatus* (Zopf, 1885) demonstrates a similar type of parasitism. The fungus, which is parasitic on the oogonia of various members of the Saprolegniae, gives rise to a sac-like structure within the oogonium from which rhizoidal hyphae are developed. *Chaetocladium* and *Parasitella* (Burgeff, 1920) show a curious form of association with members of the Mucorales, in which the fusion of the host hyphae with those of the parasite, and nuclear exchange, are outstanding features.

It is clear, therefore, that as far as fungal associations are concerned, the morphological specialisation of the parasite, except in the unusual examples *Chaetocladium* and *Parasitella*, where sexuality may at one time have been the dominant factor in the development of parasitism, is confined to the formation of appressoria and haustoria. In those parts of the fungus initiating parasitism there is a general trend from systems of unmodified lateral hyphae such as are seen in *Trichoderma* and *Papulospora*, through the stunted peg-like branches of "*Peziza*," which may be regarded as weakly differentiated appressorial developments, to the more strongly evinced haustorial organs of *Dispira, Syncephalis, Piptocephalis* and *Rhizidiomyces*.

The parasitism shown by *G. Highlei*, described in the present paper, presents features which diverge from those generally observable in the parasitism of one fungus on another. The development of an appressorium, which is undertaken by the terminal cell of the germ tube when contact is made with a *Nectria* hypha, parallels the condition described in "*Peziza*" and in *Dispira*. The development of hook cells appears, however, to be unique. Their specialised nature is emphasised by their cessation of apical growth, and by the prolific sympodial development of the mycelium of the fungus which follows from the lateral walls of the hook cells and from the appressoria and undilated hyphae at their bases. A further point in corroboration is provided by the fusion which may occur between the tip of the hook cell and the appressorium, so that the hook forms a closed collar about the parasitised hypha. *G. Highlei* appears, therefore, to develop an unusual degree of specialisation external to the host in addition to the development of an appressorium, a condition which has not so far been encountered elsewhere.

The development of specialised organs of penetration by fungal parasites appears to be correlated with the lessened effect of parasitism on the host. Where morphological specialisation is absent, the host is frequently destroyed quickly. *Trichoderma* and *Papulospora* are more rapid and complete in their effects on their hosts than is "*Peziza*," in which a certain, though weak, specialisation is developed. In *Dispira*, *Syncephalis*, *Piptocephalis* and *Rhizidiomyces* the host does not undergo rapid degeneration, but a much controlled relationship between host and parasite exists. The correlation between specialisation of the parasite and diminishing effect on the host is also of general application to the fungal parasitism of higher plants, where effects brought about by non-specialised hyphae of *Rhizoctonia*, *Botrytis* and *Pythium* may be contrasted with those produced by the haustoria-developing obligate parasites included in the Erysiphales and Uredinales (Brown, Brooks and Bawden, 1948).

The controlled host parasite relationship which accompanies specialisation is reflected in *G. Highlei*, but is not apparently correlated with the development of haustoria. In effect, the external morphological specialisation shown by the fungus seems to have replaced the internal form, whilst bringing with it a type of reaction in the host which is usually the outcome of penetration by haustorial hyphae in other cases of fungal parasitism. Parasitised *Nectria* hyphae maintain growth and reproductive activity when encumbered with a series of appressoria and hook cells, and under natural conditions in the field the parasitised *Nectria* species develop abundant perithecial stromata.

Summary.

Gonatorrhodiella Highlei A. L. Sm., a rare member of the Fungi Imperfecti only once recorded in Great Britain before, was found on the bark surfaces of stored beech and poplar logs at the Royal Botanic Garden, Edinburgh. On the beech bark the fungus was found to be associated with the perithecial stromata of *Nectria cinnabarina* (Tode) Fries., a fungus on which it has not been previously recorded, and on the poplar bark with a fungus provisionally identified as a species of *Nectria*, possessing a *Cylindrocarpon* macroconidial stage.

In culture, conidial germination of *G. Highlei* and its development of parasitism on contact with the *Nectria* sp. were observed on agars incorporating extracts obtained from *Trichoderma lignorum*, *Trichothecium roseum* and the *Nectria* species. The *Gonatorrhodiella* also grew well in the presence of the *Nectria* sp. on oatmeal mush, but no development of the fungus was observed on potato-dextrose, malt and plain agars.

The parasitism shown by the fungus involves the production of appressoria and an elaboration of hook cells of limited growth, which encircle the hyphae of the *Nectria* sp. The effect of parasitism on the *Nectria* species is slight, and results in a thinning of the hyphae at points where hook cells of the *Gonatorrhodiella* are present.

A limited growth of *G. Highlei* occurred in pure culture on oatmeal mush and on fungal extract agars. No growth occurred on potato-dextrose, malt and plain agars.

The type and development of the parasitism shown by the fungus, and the nature of its association with other fungal species, are discussed.

ACKNOWLEDGMENTS.

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EXPLANATION OF PLATES.

PLATE IV. *Gonatorrhodiella Highlei.*

Fig. 1. Conidiophores on poplar bark, seen in surface view. (Approx. × 70.)

Fig. 2. Sporiferous head of a young conidiophore, showing the terminal bulb with primary conidia (*p*), each of which bears a group of secondary conidia (*s*). (Approx. × 520.)

Figs. 3 and 4. Mature conidiophore heads showing branched chains of conidia. (Approx. × 350 and 690.)

PLATE V.

Fig. 5. Longitudinal section of the perithecial stroma of *Nectria cinnabarina* on beech, showing the mycelium of *G. Highlei* undercutting the pseudoparenchyma of the stroma at (*a*), and lying between the perithecia at (*b*). Conidiophores of *G. Highlei* are shown at (*c*). (Approx. × 250.)

Fig. 6. A conidiophore of *G. Highlei*, obtained from poplar bark, invested by hyphae of the *Nectria* species. (Approx. × 570.)

Fig. 7. Parasitism of the *Nectria* sp. (*n*) by *G. Highlei* in culture. An early stage in the development of an appressorium (*a*) and hook (*c*) by the germ tube, when contact is made with a *Nectria* hypha. (Approx. × 850.)

PLATE VI.

Fig. 8. A stage in the development of a branch hyphal system of *G. Highlei*. Distended hyphae (*h*) arise from the zone of the primary appressorium (*a*). (Approx. × 850.)

Fig. 9. A later stage in the development of a branch hyphal system of *G. Highlei*. The hyphae produced from the zone of the primary appressorium (*a*) have produced secondary hook cells (*c*) at various points on the surrounding *Nectria* hyphae (*n*). (Approx. × 850.)

Fig. 10. Paired hook cells (*c*) arising from the germ tube of *G. Highlei*. A young branch hyphal system is shown at (*a*). (Approx. × 850.)

PLATE VII.

Fig. 11. An example of the parasitism of a *Nectria* hypha (*n*) by *G. Highlei*, showing the development of a conidiophore from a hypha of the branch hyphal system of the parasite. (*a*) Extended area of the appressorium; (*c*) hook cells; (*d*) conidiophore bearing primary conidia; (*h*) hyphae of the branch hyphal system; (*o*) conidium of *G. Highlei*; (*t*) germ tube. (Approx. × 450.)

Fig. 12. Variation in the morphology of the conidiophore of *G. Highlei* when grown on fungal extract agar. The two conidiophores show limited development of the terminal bulb, and each has given rise to a single terminal, primary conidium (*p*). (Approx. × 300.)

ADDITIONS AND CORRECTIONS TO THE GENUS PRIMULA (UP TO AND INCLUDING 1949). BY WILLIAM WRIGHT SMITH and H. R. FLETCHER.

(Read 16th June 1949.)

SECTION AMETHYSTINA Balf. f.

To the paper on this section in Trans. Bot. Soc. Edin., xxxiii, 209 (1942), add this note to the introduction (pp. 209–210):

The view taken of the position of this section is subject to an important modification. Previous observations on the leaf have proved to be misleading. Recently material has been available in cultivation of three members of the section—*P. Valentiniana* Hand.-Mzt., *P. Kingii* Watt and *P. Dickieana* Watt. In these species the folding of the leaves is not involute but quite definitely revolute. The relationship therefore with sections Auricula and its allies of the Involutae cannot be upheld. The section must take its place among the Revolutae, but its position in this large series continues to be somewhat indefinite. Its nearest affinity has yet to be determined.

To **P. Dickieana** Watt add a note that the species is now in cultivation from seeds of Ludlow, Sherriff and Elliott and that cultivated plants first flowered in the Perth garden of Mr. and Mrs. J. T. Renton.

To the literature of **P. Faberi** Oliver add: Chen in Icones Omeiensium, 1, pl. 41 (1942).

To **P. Kingii** Watt add: Lowndes in Quart. Bull. Alp. Gard. Soc., xii, pl. p. 34 (1944); and this Herbarium record: Chumbi Valley, near Kaju Gompa (*Lowndes*, 759).

To **P. Valentiniana** Hand.-Mzt. add: Ludlow in Himalayan Journal, xii, fig. facing p. 4 (1942).

SECTION AURICULA Duby.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 650 (1948), make the following additions:—

To the literature of **P. Allionii** Lois. add this reference: Quart. Bull. Alp. Gard. Soc., xvi, 190, pl. p. 243 (1948); and to **P. Allionii** var. **alba** add: Quart. Bull. Alp. Gard. Soc., xvi, 142, pl. p. 153 (1948).

TRANS. BOT. SOC. EDIN., VOL. XXXV. PT. II., 1949.

To **P. auricula** Linn., **P. rubra** J. F. Gmel., and × **P. pubescens** Jacq., add this genetical account: Ernst in Arch. Klaus-Stift. Vererb-Forsch., 1, pts. 3–4, 274–453, pls. XI–XIV (1925).

To **P. auricula** Linn., **P. viscosa** All., and × **P. alpina** Schleicher add this genetical account: Ernst in Arch. Klaus-Stift. Vererb-Forsch., xv, pts. 1–2, 1–102, pls. I–II (1940).

To **P. viscosa** All. add these accounts of the genetics of heterostyly: Ernst. in Arch. Klaus-Stift. Vererb-Forsch., viii, pts. 1–2, 1–215, pls. I–VIII (1933); Ernst. *ibid.*, xi, pts. 1–2, 1–280, pls. I–III (1936); Ernst. *ibid.*, xiii, pts. 1–2, 1–381, pls. I–III (1938); Ernst. in Z. indukt. Abstamm.-u. Vererblehre, lxxi, pts. 1–2, 156–230 (1935).

SECTION BULLATAE Pax.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 454 (1946), add this reference:

To **P. Forrestii** Balf. f.: Quart. Bull. Alp. Gard. Soc., xi, 211, pl. p. 210 (1943).

SECTION CANDELABRA Balf. f.

To the paper on this section in Trans. Bot. Soc. Edin., vol. xxxiii, 122 (1941), add the following:—

To the literature of **P. Beesiana** Forrest, **P. helodoxa** Balf. f., and **P. Wilsoni** Dunn add the account of the genetics of heterostyly: Ernst in Arch. Klaus-Stift. Vererb-Forsch., xix, pts. 3–4, 265–311 (1944).

To **P. chungensis** Balf. f. et Ward, **P. Cockburniana** Hemsl., and **P. pulverulenta** Duthie add this account of the genetics of heterostyly: Ernst in Arch. Klaus-Stift. Vererb-Forsch., xviii, pts. 1–2, 87–233, pls. I–VI (1943).

To **P. japonica** A. Gray add: Quart. Bull. Alp. Gard. Soc., xi, 208, pl. p. 209 (1943).

To **P. prolifera** Wall. add the note that this species is now in cultivation from seeds collected by Dr. Bor in 1947.

This is the first authentic record of it in cultivation.

To **P. Smithiana** Craib add: Lowndes in Quart. Bull. Alp. Gard. Soc., xii, 35, pl. p. 29 (1944).

Primula sumatrana Merrill in Not. Nat. Acad. Nat. Sc. Philad., No. 47, 6 (1940).

A plant without stolons, glabrous with the exception of the inflorescence, or with the young leaves minutely and obscurely farinose; the leaves in a rosette, sessile, oblong-obovate or obovate-elliptic, rounded at the apex, 4–5 cm. long, 2–2·5 cm. broad, subcoriaceous, glabrous or in the case of the younger leaves minutely farinose on the upper side near the base, minutely dentate at the margin, generally a little revolute, somewhat narrowed below, towards the base about 1 cm. broad, subimbricate, with lateral nerves on each side about 10 in number, distinct below but somewhat obscure above. Scape erect, about 24 cm. tall, glabrous or densely sulphur-farinose at the apex; flowers erect, yellow and pale violet according to the collector, in a simple umbel, with slender pedicels; the umbels about 10-flowered, with pedicels and calyces very densely sulphur-farinose; pedicels 10–15 mm. long; bracts lanceolate, glabrous or subglabrous, 6–11 mm. long, without any gibbosity at the base. Calyx subcupulate, about 5 mm. long and 4·5 mm. broad; lobes 5–4, subtriangular-ovate, acuminate, shorter than the tube and about 2 mm. long. Corolla somewhat salver-shaped, with the tube slightly inflated above, 10–12 mm. long, glabrous, with no annulus at the throat; the lobes 5–4 in number, spreading or somewhat so, orbicular-elliptic, distinctly retuse or more rarely rotundate, 5–6 mm. long. Anthers 5–4, oblong-elliptic, 1·8 mm. long, distinctly longer than the filaments. Style slightly exserted.

SUMATRA: Atjeh, Mount Löser (*Ripley and Ulmer*, 91) 5th May 1939, at Bivouac No. 7, alt. about 2800 m.; 5th May 1939, open meadows, flowers yellow and pale violet. The type is sheet 785695 in the Herbarium of the Academy of Natural Science of Philadelphia.

The plant is represented in the Edinburgh Herbarium by a photograph of the single specimen preserved at Philadelphia. From the photograph it seems quite clear that this new species finds its nearest ally in *P. imperialis*, which is a native of Java. From this latter species it deviates in the more slender habit, in the practically sessile leaves and in the simple inflorescence. The unique specimen, judging from the photograph, would suggest that the plant represents a very dwarf form of the Javan species. But *P. imperialis* has been and continues to be in cultivation in this country and shows no indication at any time of producing dwarf forms. Although there is an approximation between the Javanese and the Sumatran species, the chances are entirely in favour of the two being quite distinct one from the other.

SECTION CAPITATAE Pax.

To the paper on this section in Trans. Bot. Soc. Edin., xxxiv, 149 (1944), add to **P. capitata** this reference: Quart. Bull. Alp. Gard. Soc., xi, 207, pl. p. 203 (1943).

SECTION CORTUSOIDES Balf. f.

To the paper on this section in Trans. Bot. Soc. Edin., xxxiv, 55 (1944), add the following:—

Primula Eugeniae Fedorov in Botanicheskii Zhurnal SSSR. (Journ. Bot. U.S.S.R.), xxxiii, 1, 31 (1948).

A perennial plant with a rhizome of several heads forming a more or less dense tuft, furnished at the top with the numerous remains of dead leaves. Leaves with long or very long petioles, reniform or subcordate in outline, obviously lobate, the lobes themselves obtuse and showing 3–5 teeth or crenatures; on the upper surface almost glabrous, below especially on the nerves softly pubescent, suddenly contracted into a slender petiole which is narrowly winged and softly pubescent; the petiole many times longer than the blade. Scapes numerous, one and a half times longer than the leaves, softly pilose. Inflorescence umbellate, glabrous, with the pedicels unequal, 2–5 times longer than the bracts. Bracts of the involucre 4–6, broad-lanceolate, acute, unequal. Flowers conspicuous, about 15–20 mm. long, often heterostyled. Calyx glabrous, campanulate, 5-fid to the middle or even beyond, with the lobes subacute and at the apex scarcely papillose. Corolla pale sulphur, three times longer than the calyx, limb somewhat flat, the lobes bilobulate at the apex, the tube subcylindric, more or less dilated at the throat and more deeply coloured. Anthers yellow inserted at the throat, subsessile, transversely 3-angled, with the filaments conoid and much shortened. Ovary rounded. Style filiform with a capitate stigma, glabrous. Seeds dark coloured or fuscous.

The author described this as a beautiful species which appears to approach more or less *P. septemloba* and at the same time seems to be somewhat apart from *P. Kaufmanniana*. It differs from both in the larger pale yellow flowers, in the form of the leaves, and in its distinct habitat as it is found in the mountains of Fergana. It occurs in clefts of limestone rocks in the high alpine region of Mt. Baubaschata of the Fergana Range in Turkestan near the snows at an altitude of 3700 metres, where the author collected it in flower in August 1945. The name is given in honour of Eugenia

Iljina who accompanied the author and made collections with him. The type specimens are preserved at Leningrad.

From an inspection of the plate which accompanies the description of this species it is clear that the association of *P. Eugeniae* is with *P. lactiflora* and *P. Kaufmanniana.* All three occur in Turkestan. The new species is marked at once by the yellow flowers—a colour very unusual in the section Cortusoides. Of the affinities quoted, *P. lactiflora* is apparently the nearest ally.

SECTION CUNEIFOLIA Balf. f.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 631 (1948), add the following reference:—

To **P. cuneifolia**: Hultén in Fl. Al. and Yukon, viii, 1269 (1948).

To **P. cuneifolia** subsp. **saxifragifolia** (Lehm.) W. W. Sm. et Forrest add the following synonym:—

P. cuneifolia subsp. *saxifragifolia* (Lehm.) Hultén in Fl. Aleut. Is., 270 (1937), and in Fl. Al. and Yukon, viii, 1269 (1948), and delete the reference Hultén in Fl. Aleut. Is., 270 (1937). The transference was previously made by W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xvi, 20 (1928).

SECTION DENTICULATA Balf. f.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 469 (1946), add the following:—

To the literature of **P. denticulata** Smith add: Quart. Bull. Alp. Gard. Soc., xiv, 72, pl. p. 68 (1946).

To **P. erythrocarpa** Craib add: Quart. Bull. Alp. Gard. Soc., xi, 208, pl. p. 206 (1943).

After *P. erythrocarpa* Craib insert the following new species:—

Primula laxiuscula W. W. Sm. Spec. nov.

Species sectionis Denticulatae atque affinis *P. atrodentatae* W. W. Sm. a qua foliis magis rotundatis pilosioribus, inflorescentiis laxis haud congestis, pedicellis evolutis, bracteis linearibus removitur; squamis basalibus deficientibus ab formis omnibus *P. denticulatae* inter alia separatur.

Perennis villosa foliis marcidis basi circumdata, rhizomate brevi sat crasso, squamis basalibus nullis. Folia petiolo incluso 2–4 cm. longa, 1–2 cm. lata, late obovata vel nunc obovato-spathulata,

apice plerumque bene rotundata, in petiolum brevum vel fere obsoletum sed interdum discretum et laminam subaequantem sensim angustata, minute crenato-dentata vel subintegra, juvenilia nunc farinosa, adulta glandulis farinipotentibus conspersa, utrinque pilis articulatis bene induta praesertim ad venas; costa atque 6–8 paria nervorum supra in sicco manifesta, infra eminentes. Scapus 4–10 cm. altus, sat robustus, supra farinosus, umbellam laxam 2–6–floram gerens, bracteis 4–5 mm. longis plerumque linearibus leviter farinosis, pedicellis 2–5 mm. longis farinosis. Calyx 5–7 mm. longus, anguste campanulatus, extra paulo farinosus vel glandulis conspersus, intus farina bene farctus, ad medium in lobos lanceolatos acutos divisus. Corolla pallido-violacea, exannulata, heteromorphica, tubo calycem duplo superante anguste cylindrico supra ampliato, limbo 1–2 cm. diametro in lobos obcordatos alte emarginatos 5–8 mm. longos et latos fisso. Stamina antheris 1·5 mm. longis paulo supra medium tubum in floribus brevistylis inserta, prope basin in floribus longistylis. Stylus longus ab ore corollino circ. 2 mm. remotus; stylus brevis circ. 2 mm. longus. Capsula calycem aequans, ceterum ut in *P. atrodentata.*

S.E. TIBET. Kongbo, Pamahochung, Tsangpo Gorge, in splash of waterfall, 10,000 ft. alt., 4.5.47 (*Ludlow, Sherriff and Elliot,* 13607—*type* in *Herb. Brit. Mus.*); open grassy hill slopes, alt. 9500 ft., 1.5.47 (*L., S. and E.*, 13588).

ASSAM HIMALAYA. Delei Valley, alt. 10,000–11,000 ft., 23.5.28 (*Kingdon Ward*, 8233, 8188).

This species is without doubt closely akin to *P. atrodentata* W. W. Sm., a plant which has been copiously collected and is now well known. One obvious distinction is the lax inflorescence with the flowers stalked. In its ally the flowers are much congested and pedicels are obsolete. The absence of basal scales among other characters distinguish it from any of the many expressions of *P. denticulata* Sm.

A very hairy perennial with a short, stout rhizome, surrounded at the base with the withered remains of old foliage, but quite devoid of basal bud scales. Leaves including the petiole 2–4 cm. long, 1–2 cm. broad at flowering time, increasing slightly in size at fruiting time, obovate to obovate-spathulate, round at the apex, tapering at the base into the broadly winged petiole, usually very short or almost obsolete, only very occasionally discrete and subequal to lamina, finely crenate-dentate or subentire at the margin, sometimes farinose on the lower surface when very young, when mature sprinkled below with potentially farinose glands, at all times

covered on both surfaces, especially along the veins, with numerous long articulate hairs; mid-rib and 6–8 pairs of lateral nerves conspicuous above, prominent below. Scape 4–10 cm. tall, sturdy and erect, farinose on the upper half, copiously so at the apex, carrying a two- to six-flowered umbel; bracts 4–5 mm. long, linear-lanceolate, faintly farinose, with a prominent mid-rib, pedicels 2–5 mm. long, farinose. Calyx 5–7 mm. long, campanulate, sprinkled with farinipotent glands, or sometimes with a little farina on the outside, obviously farinose within, cut to the middle into lanceolate acute teeth sometimes tinged with purple. Corolla pale violet, reddish brown on the tube, with a whitish-yellow eye, exannulate, heteromorphic; tube about twice the length of the calyx, narrowly cylindrical, conspicuously ampliate above the insertion of the stamens; limb 1–2 cm. in diameter with obcordate very deeply emarginate lobes 5–8 mm. long and broad. Stamens, with anthers 1·5 mm. long, inserted just above the middle of the corolla tube in thrum-eyed flowers, near the base of the tube in pin-eyed. Long style reaching to within 2 mm. of the mouth of the corolla tube; short style 2 mm. long. Capsule as long as the calyx, dehiscing by longitudinal valves.

SECTION FARINOSAE Pax.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 1 (1943), there are several additions:

To **P. auriculata** Lam. add this reference: Czeczott, Fl. of Turkey, 208 (1939).

To **P. blandula** W. W. Sm. add: Bruun, Cytological Studies in Primula, 49, 128 (1932)—which indicates that the plant was in cultivation for a brief period from Ward's seed.

To **P. borealis** Duby add the following references: Gray, Synopt. Fl. N. Am., ii, 1, 58 (1878); Macoun, Cat. Can. Pl., ii, 310 (1884)—*pro parte*; Nelson, Rep. Hist. Nat. Coll. Alaska, 30, 31 (1887); Muir, Cruise of Corwin, 287, 291 (1917); Hutch. N. Rime-Ringed Sun, 255 (1934); Gröntved in Fifth Thule Exp., 80 (1936); Pors. in Rhodora, xli, 276 (1939); Hultén, Fl. Al. and Yuk., viii, 1268 (1948).

Add also this note:

Hultén treats *P. ajanensis* Busch as a variety of *P. borealis* Duby. Apparently he has seen no specimens. *P. ajanensis* is no close ally of *P. borealis*. We have examined the type specimen and find that it is equivalent to *P. Matsumurae* Petitm. (see under *P. Matsumurae* in Trans. Roy. Soc. Edin., lxi, 28). Thus *P. borealis* var. *ajanensis* (Busch) Hultén becomes a synonym of *P. Matsumurae.*

Hultén also follows some other authors in retaining *P. parvifolia* Duby as distinct from *P. borealis.* In Trans. Roy. Soc. Edin., lxi, 8, Smith and Fletcher treat *P. borealis* and *P. parvifolia* at considerable length. They came to the conclusion that *P. parvifolia* is equivalent to *P. borealis.* These two plants have been held as distinct by Fernald, and later by Hultén (Fl. Al. and Yukon, 1268). Very ample material has been received in Edinburgh collected at one place by Miss Ruth Reat, in 1944, in the vicinity of Nome. This material shows typical *P. borealis.* Along with it are specimens which agree with what has been called by various authors *P. parvifolia.* The distinction usually relied on is the broad corolla of *P. borealis* as opposed to the narrow and very segmented corolla lobes of *P. parvifolia.* In the Reat material there is a complete transition from one to the other. Not only so, but in one or two specimens where the scape is two-flowered, one flower has the corolla of *P. borealis* and the other the corolla of *P. parvifolia.* We therefore regard the problem as solved. We have also received the privilege of the loan from New York of the one sheet extant of *P. tenuis* Small. From the description we formed the opinion (Trans. Roy. Soc. Edin., lxi, 9) that *P. tenuis* was probably equivalent to some condition or other of *P. borealis.* The type material of *P. tenuis* is very limited but there remains no doubt but that it is equivalent to *P. parvifolia* and thus to *P. borealis.* Smith and Fletcher (*loc. cit.*) also mention specimens collected at Nome by Miss Hutchison. These are in the Kew Herbarium as *P. stricta,* and are referred to by Hultén (*loc. cit.*, 1274). We cannot reconcile these specimens with *P. stricta.* They appear again in Miss Reat's collection along with *P. borealis* and its equivalent *P. parvifolia*; and appear to represent a still more reduced form of what has been called *P. parvifolia.* Further material, including seeds, is being sought from Nome, where apparently typical *P. borealis,* with its variant *P. parvifolia,* as well as the peculiar dwarf *P. tenuis,* are to be found in the one neighbourhood.

P. borealis is recorded also from Saghalin. It is so given by Miyabe and Tatewaki in Trans. Sapporo Nat. Hist. Soc., xiv, 78 (1935). A little later the Saghalin plant was given specific rank by Hara under the name *P. Kawasimae* in Journ. Jap. Bot., xvii, No. 11, 633 (1941). In his description Hara differentiates the Saghalin plant from *P. borealis* Duby but makes no mention whatever of *P. parvifolia* Duby. He also cites a white-flowered variety of the same plant. We have seen no authentic material collected in Saghalin, but the description given does not appear to give any criteria of moment which would serve to distinguish it from one of the many forms of *P. borealis*. We would be inclined to agree with the identification first given to it by Miyabe and his colleague.

Accordingly to the synonymy of *P. borealis* add: ? *P. Kawasimae*. Journ. Jap. Bot., xvii, No. 11, 633 (1941).

To **P. Clarkei** Watt add the reference: H. R. Fletcher, Bot. Mag., t. 17 (1948).

To **P. Comberi** W. W. Sm. add: Lourteig in Darwinia, vii, 558, (1947).

To **P. egaliksensis** Wormsk. add the following synonym: *P. egaliksensis* Hultén in Fl. Al. and Yukon, viii, 1271 (1948).

To **P. Fauriae** Franch. add the following distribution:—

JAPAN. Honshu: Prov. Iwaki, Mt. Omaidake (*S. Saito* in 1931). Kuriles: I. Shikotan (*K. Kondo* in 1929; *S. Saito* in 1925).

To the herbarium record of **P. glabra** Klatt add: Chumbi Valley, Nathu La (*Lowndes*, 746).

To the literature of **P. Halleri** J. F. Gmel. add, under the synonym *P. longiflora* All., the following reference: Ernst in Veröff. geobot. Inst. Rübel., iii, 628–654 (1925).

To **P. incana** Jones add these references: Pors. in Rhodora, xli, 277 (1939); Hultén in Fl. Al. and Yukon, viii, 1272 (1948).

To **P. involucrata** Wall. add: Quart. Bull. Alp. Gard. Soc., xi, 208, pl. p. 209 (1943).

To **P. macrocarpa** Maxim. add this distribution:

JAPAN. Honshu: Prov. Rikuchu, Mt. Hayachine (*Hara* in 1932).

To **P. magellanica** Lehm. add the following synonyms: *P. farinosa* var. *magellanica* (Lehm.) Hook. f.; Lourteig in Lilloa, viii, 236 (1942). *P. farinosa* subsp. *magellanica* (Hook. f.) W. W. Sm. et Forrest in Notes Roy. Bot. Gard. Edin., xvi, 24 (1928), and in Journ. Roy. Hort. Soc., liv, 32 (1929); Becherer in Verh. Nat. Gespellsch. Basel, lvi, 171 (1945); Lourteig in Darwinia, vii, 557 (1947).

To **P. Matsumurae** Petitm. add this synonym: *P. borealis* var. *ajanensis* (Busch) Hultén in Fl. Al. and Yukon, viii, 1268 (1948).

To **P. mistassinica** Michx. add the reference: Hultén in Fl. Al. and Yukon, viii, 1272 (1948).

To **P. modesta** Bisset et Moore add the following distribution:—

JAPAN. Honshu: Prov. Kodzuke, Mt. Shibutsu (*S. Saito*). Mt. Tanigawa-Lake (*Hara* in 1932).

To **P. pulchella** Franch. add this extension in distribution:

S.E. TIBET. Nambu La (*Ludlow, Sherriff and Elliot*, 15789).

To **P. sibirica** Jacq. add the following references: Pors. in Rhodora, lxi, 277 (1939); Hultén in Fl. Al. and Yukon, viii, 1273 (1948).

To **P. sibirica** Jacq., under the synonym *P. finmarchica* Jacq., add the reference: E. Christophersen in Nytt Mag. Naturv., lxxxi, 13 (1941), where the view is expressed that *P. finmarchica* is a plant of the shore, and thus may be regarded as differing, ecologically, from the steppe and mountain plant *P. sibirica*.

To **P. specuicola** Rydb. add this reference and note: Kearney and Peebles, Flowering Plants and Ferns Arizona, 666 (1942). These authors quote *Eastwood and Howell*, 1024, from the North rim of the Grand Canyon. They point out that the type of *P. Hunnewellii* Fernald also came from the Grand Canyon and suggest that it is only a state of *P. specuicola*.

To this species also add this distributional and herbarium record:

UTAH. Sheep Canyon, 2 miles up S. side of Colorado R. from bridge. Moab (*C. R. Worth*, 353).

To **P. stricta** Hornem. add this reference: Hultén in Fl. Al. and Yukon, viii, 1274 (1948).

To **P. Tayloriana** H. R. Fletcher in Journ. Roy. Hort. Soc., lxxiv, 210, fig. 70 (1949), add the English description:

A farinose perennial with a short fairly thick rootstock from which spring numerous fibrous roots and which is crowned with a farinose resting-bud at most 1 cm. long. Leaves obovate, 4–5 cm. long including the petiole, 2–3 cm. broad, round at the apex, tapering at the base into the petiole which is hardly separable from the lamina, denticulate or crenate-denticulate at the margin, glabrous, efarinose above, covered below except on the main nerves with cream-coloured farina, mid-rib and 6–8 pairs of lateral nerves conspicuous above, prominent below. Scape 4–10 cm. tall, fairly stout, obviously farinose at the apex and sprinkled with farina elsewhere, carrying an umbel of 2–8 flowers; bracts 3–7 mm. long, linear to linear-lanceolate, sparingly farinose, keeled towards the base; pedicels 5–15 mm. long, farinose. Calyx 5–7 mm. long, campanulate, farinose, cut to two-thirds into lanceolate acute lobes each with one prominent vein. Corolla violet with a whitish-yellow eye, exannulate, heteromorphic; tube narrowly cylindrical, 2–3 times the length of the calyx; limb 2–2·5 cm. in diameter with obcordate, deeply emarginate lobes. Stamens, with anthers 2 mm. long inserted at the apex of the corolla tube in thrum-eyed flowers, near the middle of the tube in pin-eyed. Long style as long as corolla tube or obviously exserted, short style half the length of the corolla tube. Capsule oblong, a little longer than calyx, dehiscing by longitudinal valves.

To **P. yargongensis** Petitm. add this reference: Quart. Bull. Alp. Gard. Soc., x, 226, pl. p. 227 (1942).

SECTION FLORIBUNDAE Pax.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 637 (1948), add to the literature quoted in the introduction the following reference to the genetics of the species:—

Ernst in Archiv der Julius Klaus-Stiftung., xxiv, 17–104 (1949).

SECTION MALACOIDES Balf. f.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 444 (1946), add this reference:

To **P. Forbesii** Franch: Addisonia, xxii, pl. 736 (1947).

SECTION MINUTISSIMAE Pax.

To the paper on this section in Trans. Bot. Soc. Edin., xxxiii, 227 (1942), add the following:—

Primula candicans W. W. Sm. Spec. nov.

Species sectionis Minutissimarum atque affinis *P. rimicolae* W. W. Sm. et *P. spathulifoliae* Craib; a priore foliis apice magis rotundatis minus conspicue denticulatis albo-farinosis, scapo breviore foliis immerso, tubo corollino magis elongato angustiore, staminum insertione divergit; ab altera foliis forma texturaque serraturaque diversis, scapo haud obsoleto inter alia recedit.

Perennis caespitosa 2·5–3 cm. alta, foliis emarcidis basi circumdata, rhizomate brevi satis robusto nunc ramoso. Folia rosulatim compacta, petiolo incluso 2–3 cm. longa, 0·5–1·5 cm. lata, obovata vel oblanceolata vel nunc spathulata, plerumque apice subrotundata vel nonnunquam acutata, in petiolum alatum laminae subaequalem sensim angustata, supra medium minute denticulata infra subintegra, farina alba supra conspersa infra densius; costa atque 4–6 paria nervorum subtus manifesta. Scapus foliis occultus 1 cm. haud excedens, farinosus, florem solitarium vel nunc umbellam 2–4-floram gerens, bracteis 5–7 mm. longis linearibus vel lineari-lanceolatis farinosis, pedicellis 5–10 mm. longis serius paulo elongatis. Calyx 8 mm. longus anguste campanulatus vel potius subcylindricus, viridis, farinosus, ad tres partes in lobos lanceolatos acutos partitus. Corolla exannulata, heteromorphica, violacea, extra farina conspersa, tubo calycem duplo vel triplo superante anguste cylindrico, oculo albo, limbo 1–2 cm. diametro in lobos ad 1 cm. longos et latos obcordatus alte emarginatos diviso. Stamina antheris 1 mm. longis ad medium tubum in floribus longistylis inserta, ad apicem in floribus brevistylis. Stylus longus ad os pertinens; brevis medium tubum aequans. Capsula e calyce vix exserta.

S.E. Tibet. Pome, Sobhe La, near Tongyub Dzong, abundant on rock faces, alt. 12,500 ft., 21.5.47 (*Ludlow, Sherriff and Elliot*, 13749—*type* in *Herb. Brit. Mus.*); Pome, Sobhe La, 13,500 ft., 5.4.47 (*L., S. and E.*, 15341).

The nearest ally of this species appears to be another Tibetan plant, *P. rimicola* W. W. Sm., from which it differs in the foliage, the farina and the flower structure. More remote is the Sikkim species, *P. spathulaefolia* Craib, where the leaf characters are quite distinctive.

A dwarf tufted perennial with a short, stout, sometimes branching rhizome and covered at the base by the withered remains of old foliage. Leaves forming a compact rosette, obovate or oblanceolate to spathulate, 2–3 cm. long including the petiole, 0·5–1·5 cm. broad, usually more or less rounded at the apex, tapering into the membraneously winged petiole subequal to lamina, minutely denticulate at the margin in the upper half, elsewhere subentire, sprinkled with farina above, covered with abundant cream or pale yellow farina below; mid-rib and 4–6 pairs of lateral nerves not conspicuous above, prominent below. Scape hidden among the foliage at most 1 cm. long, 1 or 2 to a plant, conspicuously farinose, carrying a single flower or a 2–4 flowered umbel; bracts linear or linear-lanceolate, 5–7 mm. long, farinose; pedicels 5–10 mm. long, slightly elongating at fruiting-time, farinose. Calyx narrowly campanulate to cylindric, 8 mm. long, sage-green, farinose, cut to three parts of its length into lanceolate acute lobes each with a prominent mid-rib. Corolla violet with tube greenish and streaked longitudinally with dark lines and with white eye, faintly farinose without, exannulate, heteromorphic; tube 2–3 times the length of calyx, very narrowly cylindrical; limb 1–2 cm. diameter with obcordate, deeply emarginate lobes up to 1 cm. long and broad. Stamens, with anthers 1 mm. long inserted at the middle of the corolla tube in pin-eyed flowers, at the apex of the tube in thrum-eyed. Long style reaching the mouth of the corolla tube; short style half the length of tube. Capsule barely as long as the calyx dehiscing by longitudinal valves.

To **P. flagellaris** W. W. Sm. add the following references: Quart. Bull. Alp. Gard. Soc., vii, 215, pl. p. 210 (1939); Sherriff and Taylor, *ibid.*, viii, 113, pl. p. 107 (1940).

To **P. pusilla** Wall. add: Sherriff and Taylor in Quart. Bull. Alp. Gard. Soc., viii, 114, pl. 110 (1940), and this Herbarium record:

SIKKIM. Nathu La (*Lowndes*, 760).

To **P. rimicola** W. W. Sm. add the following reference and note: Cooke in Quart. Bull. Alp. Gard. Soc., xii, 134, fig. p. 138 (1944).

Mr. R. B. Cooke flowered this plant for the first time in cultivation in 1944, from seeds of *Ludlow and Sherriff*, 3897.

Primula rubicunda H. R. Fletcher. Spec. nov.

Species sectionis Minutissimarum atque affinis *P. annulatae* Balf. f. et Ward et *P. Stirtonianae* Watt; a priore floribus duplo majoribus, corollae tubo e calyce bene exserto divergit; ab altera scapo folia longe superante haud immerso, corollae tubo prominenter annulato recedit; quoad folia species omnes tres sunt fere similes.

Planta perennis caespitosa efarinosa circ. 2 cm. alta, basi reliquiis foliorum emarcidorum circumdata, rhizomate brevi tenui nunc ramoso. Folia rosulatim compacta; lamina petiolo incluso 7–15 mm. longa, 3–5 mm. lata, obovata vel spathulata, apice ambitu rotundata sed margine ubique crenato-dentata vel dentata, basi in petiolum alatum subaequantem angustata, utrinque glandulis minutis farinipotentibus faciem scabridam efficientibus induta; costa media cum nervis 3–4-paribus supra obscura, infra eminens. Scapus 1–2 cm. altus, tenuiter glandulosus, florem erectum unicum gerens, bracteis binis 1–2 mm. longis linearibus, pedicellis 2–3 mm. longis. Calyx 3–4 mm. longus, campanulatus, viridis, sub lente glandulosus, fere ad medium in lobos ovatos vel lanceolatos acutos vel nunc obtusos fissus. Corolla roseo-rubicunda, distincte annulata, heteromorphica; tubus calyce paulo longior vel nunc fere duplo superans; limbus 1·5 cm. diametro, lobis obovatis alte bilobulatis. Stamina, antheris vix 1 mm. longis, in floribus longistylis circ. 1·5 mm. supra basim tubi corollini inserta, in floribus brevistylis prope apicem. Stylus longus ad annulum 10-lobatum pertinens, brevis tubum medium aequans. Capsula calyce paulo exserta valvis longitudinalibus dehiscens. Semina desunt.

S.E. TIBET. Pome, Nambu La, Tongyuh River, growing on earth or rock faces; alt. 14,500 ft., 5.6.47 (*Ludlow, Sherriff and Elliot*, 13852—*type* in *Herb. Brit. Mus.*).

This Tibetan plant finds its nearest allies in *P. Stirtoniana* Watt from Sikkim and Bhutan and in *P. annulata* Balf. f. et Ward from that part of W. Yunnan which is just outside Tibet. *P. rubicunda* is readily distinguished from the former by the well-developed scape and from the latter by the much larger flowers. The foliage characters of the three are somewhat similar.

A dwarf efarinose perennial about 2 cm. tall, with a short, thin, sometimes branching rhizome and with the base covered by the remains of old leaves. Leaves forming a compact rosette; obovate to spathulate, 7–15 mm. long including the petiole, 3–5 mm. broad, round at the apex, deeply crenate-dentate to dentate at the margin, tapering at the base into the winged petiole subequal to the lamina, covered above and below with potentially farinose glands giving the leaves a scabrid appearance; mid-rib and 3–4 pairs of lateral nerves obscured above, prominent below. Scape 1–2 cm. tall, thinly covered with potentially farinose glands, carrying a solitary erect flower; bracts 2, linear, 1–2 mm. long; pedicels 2–3 mm. long. Calyx green, campanulate, 3–4 mm. long, covered with potentially farinose glands, cut to the middle, or almost so, into ovate to lanceolate, acute or obtuse lobes. Corolla pinkish red, annulate, heteromorphic; tube a little longer than the calyx or nearly twice as long; limb 1·5 cm. in diameter with obovate bilobulate lobes. Stamens, with anthers barely 1 mm. long, inserted about 1·5 mm. above the base of the corolla tube in pin-eyed flowers, near the apex of the tube in thrum-eyed. Long style reaching the very conspicuous 10-lobed annulus, short style about half the length of the corolla tube. Capsule only a little longer than the calyx dehiscing by longitudinal valves. Seeds . . .

To **P. Stirtoniana** Watt add this reference: Sherriff and Taylor in Quart. Bull. Alp. Gard. Soc., viii, 113, pl. p. 102 (1940).

To **P. tenella** King ex Hook. add: Sherriff and Taylor in Quart. Bull. Alp. Gard. Soc., viii, 117, pl. p. 115 (1940).

SECTION MUSCARIOIDES Balf. f.

To the paper on this section in Trans. Bot. Soc. Edin., xxxiii, 273 (1943), add:

To **P. apoclita** Balf. f. et Forrest this reference: Quart. Bull. Alp. Gard. Soc., xi, 207, pl. p. 204 (1943).

To **P. hyacinthina** W. W. Sm. add: Quart. Bull. Alp. Gard. Soc., x, 243, pl. p. 245 (1942); *ibid.*, xi, 207, pl. p. 204 (1943).

SECTION NIVALES Pax.

To the paper on this section in Trans. Roy. Soc. Edin., lx, 563 (1942), add:

To **P. chionantha** Balf. f. et Forrest this reference: Quart. Bull. Alp. Gard. Soc., ix, 329, pl. p. 322 (1941).

To **P. elongata** Watt add: Lowndes in Quart. Bull. Alp. Gard. Soc., xii, pl. p. 33 (1944).

To **P. Farreriana** Balf. f. add: Quart. Bull. Alp. Gard. Soc., i, 197, pl. XCVII (1932).

To **P. macrophylla** var. **Moorcroftiana** (Wall.) Pax, under the synonym of *P. Moorcroftiana* add: Quart. Bull. Alp. Gard. Soc., xiv, 73, 99, pl. p. 137 (1946).

To **P. nivalis** Pallas add the following reference and note: Hultén in Fl. Al. and Yukon, viii, 1272 (1948).

Smith and Fletcher have not recorded this species from the American side of the Bering Straits. But Hultén mentions a specimen agreeing with Altai material, obtained by Wales Anderson in the Bering Strait district. This locality appears to be a vague term. Does *P. nivalis* occur in American territory?

To **P. obliqua** W. W. Sm. add the following references: Sherriff and Taylor in Quart. Bull. Alp. Gard. Soc., viii, 118, pl. p. 116 (1940); Lowndes, *ibid.*, xii, 28, pl. p. 33 (1944).

To **P. obtusifolia** Royle add: Quart. Bull. Alp. Gard. Soc., xv, 7, pl. p. 6 (1947).

To **P. Tschuktschorum** Kjellm. add: Hultén in Fl. Al. and Yukon, viii, 1275 (1948)—*pro parte.*

To **P. Tschuktschorum** var. **arctica** Fernald add this synonym: *P. eximia* Hultén in Fl. Aleut. Islands, 272 (1937).

SECTION OBCONICA Balf. f.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 415 (1946), add this distributional and herbarium record to **P. filipes** Watt:

MANIPUR STATE (*Kingdon Ward*, 17236).

SECTION PARRYI W. W. Sm.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 644 (1948), add this reference:

To **P. Ellisiae** Pollard et Cockerell: Quart. Bull. Alp. Gard. Soc., xi, 207, pl. p. 206 (1943).

SECTION PETIOLARES Pax.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 271 (1944), add the following:—

To **P. aureata** Fletcher add these references and note: Quart. Bull. Alp. Gard. Soc., xv, 218, pl. p. 220 (1947); Curtis and Hay, New Plants of the Year, 93, pl. p. 96 (1948).

This species set ripe capsules with Mr. Livingstone of Carluke in August 1948. A few seeds germinated and Mr. Livingstone pricked off two seedlings on 1st August 1949.

To **P. bhutanica** Fletcher add the references: Quart. Bull. Alp. Gard. Soc., xi, 103, pl. p. 101 (1943); *ibid.*, xiv, 105, 120, 124, pl. p. 126 (1946).

To **P. Boothii** Craib add this note:

Plants raised from seeds collected in the Eastern Himalaya under the name *P. petiolaris* Wall. are now in cultivation and appear to represent exactly this species. It is certainly very closely allied to *P. scapigera* Craib and, like this species, is propagated readily by leaf cuttings.

To **P. Calderiana** Balf. f. et Cooper add the reference: Quart. Bull. Alp. Gard. Soc., xii, 32, pl. p. 36 (1944)—and the note that it has been successfully crossed with *P. tsariensis* W. W. Sm.

After *P. scapigera* Craib insert the following hybrids:—

× **P. Pandora** Hort.: Journ. Roy. Hort. Soc., lxvii, proc. p. xxxv (1942); *ibid.*, lxix, 180, proc. p. xxxiii (1944); Quart. Bull. Alp. Gard. Soc., xii, 78, pl. p. 79 (1944).

♀ *P. scapigera* × ♂ *P. Edgeworthii* is the parentage of this hybrid which was raised by Mrs. C. B. Saunders, of Farnborough, Kent, in March 1942. The flowers are of bishop's violet (H.C.C., 34), with a yellow and white eye and are produced in great freedom. It received the Award of Merit in 1944.

× **P. scapeosa** Hort.: Journ. Roy. Hort. Soc., lxxii, 374, proc. p. lii (1947); Quart. Bull. Alp. Gard. Soc., xv, 138, pl. p. 139 (1947); Curtis and Hay, New Plants of the Year, 97, pl. p. 98 (1948).

♀ *P. scapigera* × ♂ *P. bracteosa* is the parentage of this fine hybrid, raised by Mr. R. B. Cooke of Corbridge, Northumberland. The flowers are a solferino-purple (H.C.C., 26/2), with a prominent yellow eye surrounded by a clearly marked white ring. Mr. Cooke received the Award of Merit for his hybrid in March 1947.

To the literature of **P. sonchifolia** Franch. add: Quart. Bull. Alp. Gard. Soc., xvii, 110, pl. p. 107 (1949).

SECTION PINNATAE R. Knuth.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 442 (1946), add:

P. ranunculoides Chen in Notes Roy. Bot. Gard. Edin., xx, 120, pl. CCLIX (1948).

A small fragile efarinose perennial 7–10 cm. tall, with a very slender rhizome. Leaves very thinly membranaceous in texture, glabrous, covered on the lower surface with numerous small glandular striae, dimorphic; the first leaves simple, 3 4 cm. long including the petiole, with the ovate lamina about 1 cm. long and broad and deeply dentate; later leaves pinnate and up to 8 cm. long with the terminal leaflet up to 1·5 cm. long and broad, and the lateral leaflets much smaller and all grossly dentate. Scape about 7 cm. tall, filiform, carrying a 2–4-flowered umbel; pedicels very thin and slender, 2–3 cm. long; bracts linear, 1–2 mm. long. Calyx 5 mm. long, narrowly campanulate, glabrous, cut to well below the middle into linear-lanceolate lobes. Corolla exannulate?, heteromorphic, purplish, infundibuliform; tube twice as long as the calyx, narrowly cylindrical; limb 1·5–2 cm. in diameter, with obcordate, slightly emarginate lobes. Stamens in short-styled flowers inserted near the mouth of the corolla tube; style as long as the calyx. Capsule not seen.

China. Near Wuling Hsien, East Kiangsi—at Ying Nu, Tang Tung Tze Temple, on marshy ground near the pond; 27th March 1946 (*Hsiung*, 1000). In Herb. Lu Shan and in Edinburgh.

SECTION REINII Balf. f.

To the paper on this section in Trans. Roy. Soc. Edin., lxi, 437 (1946), add:

To **P. tosaensis** Yatabe this reference: Quart. Bull. Alp. Gard. Soc., xi, 211, pl. p. 210 (1943).

SECTION SIKKIMENSIS Balf. f.

To the paper on this section in Trans. Bot. Soc. Edin., xxxiii, 431 (1943), make the following additions:—

To the literature of **P. Florindae** Ward add: Quart. Bull. Alp. Gard. Soc., xi, 208, pl. 205 (1943).

To **P. ioessa** var. **subpinnatifida** (W. W. Sm.) W. W. Sm. et Fletcher add the note that it received an Award of Merit at the Chelsea Show, 1949, when exhibited by Col. Knox Finlay, Keillour Castle, Methven, Perthshire.

To the literature of **P. reticulata** Wall. add: Lowndes in Quart. Bull. Alp. Gard. Soc., xii, pl. p. 36 (1944), and this Herbarium record:

SIKKIM. Changu (*Lowndes*, 740).

To the literature of **P. sikkimensis** Hook. add: Quart. Bull. Alp. Gard. Soc., xi, 208, pl. p. 205 (1943).

SECTION SOLDANELLOIDEAE Pax.

To the paper on this section in Journ. Linn. Soc., lii, 321 (1942), make the following additions:—

To **P. chasmophila** Balf. f. ex Hutchinson add the reference: Sherriff and Taylor in Quart. Bull. Alp. Gard. Soc., viii, 114, pl. p. 108 (1940).

To **P. Reidii** Duthie add this distributional record:

KASHMIR. Sinthan Pass (*Ludlow*, 180).

To **P. Sherriffae** W. W. Sm. add this distributional and Herbarium record:—

MANIPUR STATE. Extreme summit of Sirhoi Kashong (*Kingdon Ward*, 17616).

Known previously only from S.E. Bhutan, distant 250 miles across the whole width of the Assam valley. Ward records the plant (Journ. Roy. Hort. Soc., lxxiv, 335, 1949) growing in such profusion that: "Though visibility never exceeded a hundred yards, we spied a cliff which was so closely plastered with *P. Sherriffae* that it loomed up in the mist like the White Cliffs of Dover."

To **P. soldanelloides** Watt add this distributional note: Foot of Nathu La (*Lowndes*, 762). Lowndes remarks on the frequent presence of twin flowers tinged with purple.

To **P. umbratilis** Balf. f. et Cooper add the references: Sherriff and Taylor in Quart. Bull. Alp. Gard. Soc., viii, 114, pl. p. 109 (1940); *ibid.*, ix, 151, pl. p. 149 (1941): and

To **P. umbratilis** var. **alba** Fletcher add: Quart. Bull. Alp. Gard. Soc., vii, 215, pl. p. 214 (1939).

After *P. Wollastonii* Balf. f. add:

P. Wollastonii × **P. Reidii,** Quart. Bull. Alp. Gard. Soc., xv, 8, pl. p. 9 (1947).

This cross was made by Mr. R. B. Cooke in 1944. From the resulting seeds, which were sown in 1945, plants were flowered in 1946. In most respects this hybrid is intermediate between, and a more vigorous grower than the parents.

SECTION SOULIEI Balf. f.

To the paper on this section in Trans. Bot. Soc. Edin., xxxiii, 459 (1943), add the following:—

To **P. rupicola** Balf. f. et Forrest add the reference: W. W. Sm. in Bot. Mag., t. 9683A (1948).

SECTION VERNALES Pax.

To the paper on this section in Trans. Bot. Soc. Edin., xxxiv, 402 (1947), add this hybrid of *P. elatior*:

P. elatior (L.) Hill × **veris** L. × **vulgaris** Huds. = **P. elatior** (L.) Hill × **P. variabilis** Goup =

× **P. Murbeckii** B. Lindquist in Bot. Not., 701–710 (1939).

A native of the Danish island of Moen, this plant combines the foliage characters mostly of *P. elatior* with flowers that are intermediate between *P. elatior* and *P. variabilis*.

ADDENDUM.

All the sections of Primula have now received monographic treatment and the publications concerned are as follows:—

Trans. Roy. Soc. Edin.

Nivales	lx, pt. ii, No. 17, 563–627 (1942).
Farinosae	lxi, pt. i, No. 1, 1–69 (1943).
Petiolares	lxi, pt. ii, No. 10, 271–314 (1944).

Obconica	lxi, pt. ii, No. 17, 415–478 (1946).
Sinenses	
Reinii	
Pinnatae	
Malacoides	
Bullatae	
Carolinella	
Grandis	
Denticulata	
Cuneifolia	lxi, pt. iii, No. 22, 631–686 (1948).
Floribundae	
Parryi	
Auricula	

Trans. Bot. Soc. Edin.

Candelabra	xxxiii, pt. ii, 122–181 (1941).
Amethystina	xxxiii, pt. iii, 209–294 (1942).
Minutissima	
Bella	
Muscarioides	
Sikkimensis	xxxiii, pt. iv, 431–487 (1943).
Souliei	
Rotundifolia	
Cortusoides	xxxiv, pt. i, 55–158 (1944).
Malvacea	
Pycnoloba	
Dryadifolia	
Capitatae	
Vernales	xxxiv, pt. iv, 402–468 (1948).

Journ. Linn. Soc.

Soldanelloideae	lii, No. 344, 321–335 (1942).

APPENDIX.

When this paper was ready for the press we received a copy of the first part of Hiroshi Hara's long-awaited *Enumeratio Spermatophytarum Japonicarum*, published in December 1948. This part of the *Enumeratio* contains Hara's list of the Japanese Primulas. We deem it advisable to append to this paper this enumeration and interpretation of the species of Japan by a modern Japanese botanist.

P. cuneifolia Ledeb. var. **typica** Makino.

P. cuneifolia f. **leucantha** Hara, nom. nov.

Hara regards as synonymous *P. cuneifolia* var. *albiflora* Koidz. Koidzumi's plant was recorded by Smith and Fletcher (Trans. Roy. Soc. Edin., lxi, 634, 1948) as being equivalent to *P. cuneifolia* subsp. *saxifragifolia* (Lehm.) W. W. Sm. et Forrest. Evidently Hara does not recognise this subspecies as a Japanese plant. The references therefore to this subspecies in Smith and Fletcher should not include the citations from Tokyo Bot. Mag. and other Japanese publications. Hara refers the Japanese plant to *P. cuneifolia* form. *leucantha* Hara.

P. cuneifolia var. **hakusanensis** (Franch.) Makino. Regarded as a subsp. of *P. cuneifolia* by Smith and Fletcher (*l.c.*).

P. cuneifolia var. **hakusanensis** form. **alba** Hara, nom. nov.

P. cuneifolia var. **heterodonta** (Franch.) Makino. Regarded as a subsp. of *P. cuneifolia* by Smith and Fletcher (*l.c.*).

P. cuneifolia var. **heterodonta** form. **nivea** Hara, nom. nov.

P. cuneifolia var. **tanigawensis** Tatewaki. Reduced to *P. cuneifolia* by Smith and Fletcher (*l.c.*).

P. nipponica Yatabe.

P. hidakana Miyabe et Kudo.

P. hidakana var. **kamuiana** (Miyabe et Tatew.) Hara, comb. nov.

This plant was retained with doubt as a species by Smith and Fletcher (Trans. Roy. Soc. Edin., lxi, 439, 1946).

P. kitadakensis Hara. (Syn. *P. Hisauchii* Miyabe et Tatewaki.) Reduced to *P. Reinii* Franch. et Savatier by Smith and Fletcher (*l.c.*, 439).

P. Okamotoi Koidzumi. Also reduced by Smith and Fletcher to *P. Reinii* (*l.c.*, 439).

P. Reinii Franch. et Savatier.

P. Reinii form. **albiflora** Makino.

P. Takedana Tatewaki.

P. tosaensis Yatabe.

P. tosaensis form. **brachycarpa** Hara. (Syn. *P. senanensis* Koidz. Regarded as synonymous with *P. tosaensis* by Smith and Fletcher (*l.c.*, 441).

P. japonica A. Gray.

P. jesoana Miquel.

P. jesoana var. **pubescens** (Takeda) Takeda et Hara, **P. jesoana** var. **pubescens** form. **albiflora** Tatewaki and form. **nudiuscula** (Nakai et Kitagawa) Hara; **P. jesoana** var. **glabra** (Takeda) Takeda et Hara; **P. jesoana** var. **glabra** form. **leucantha** Hara; all reduced to *P. jesoana* by Smith and Fletcher (Trans. Bot. Soc. Edin., xxxiv, 94, 1944).

P. kisoana Miquel and var. **shikokiana** Makino; the latter regarded as synonymous with *P. kisoana* by Smith and Fletcher (*l.c.*, 98).

P. Sieboldii E. Morren; form. **lactiflora** (Nakai) Hara; form. **spontanae** Takeda; form. **hortensis** Takeda. All these forms Smith and Fletcher reduced to the synonymy of *P. Sieboldii* (Trans. Bot. Soc. Edin., xxxiv, 81, 1944).

P. Sieboldii form. **incisa** (Miq.) Makino.

P. farinosa Linn. var. **xanthophylla** Trautvetter et Meyer.

P. Kawasimae var. **albiflora** Hara.

P. macrocarpa Maxim.

P. modesta Bisset et Moore var. **genuina** Takeda; var. **ajanensis** (E. Busch.) Hara; var. **Fauriae** (Franch.) Takeda; var. **Matsumurae** (Petitm.) Takeda. In the *P. modesta* complex Smith and Fletcher (Trans. Roy. Soc. Edin., lxi, 1943) preferred, rather dubiously, to retain as species *P. Matsumurae* (*l.c.*, 28) and *P. Fauriae* (*l.c.*, 18). Having seen the type of *P. ajanensis*, Smith and Fletcher do not consider it entitled to varietal rank and reduce it to *P. Matsumurae.*

P. modesta var. **Fauriae** form. **leucantha** Hara, nom. nov.

P. modesta var. **Matsumurae** form. **alba** Hara, nom. nov.

P. modesta var. **samanimontana** (Tatewaki) Nakai. Regarded by Smith and Fletcher (*l.c.*, 18) as synonymous with *P. Fauriae.*

P. modesta var. **samanimontana** form. **nivea** Hara, nom. nov.

P. sachalinensis Nakai. Reduced by Smith and Fletcher to *P. farinosa* var. *xanthophylla* Trautv. et Meyer (*l.c.*, 18).

P. sibirica Jacq.

P. sorachiana Miyabe et Tatewaki.

P. yuparensis Takeda.

P. Tschuktschorum Kjellman var. **arctica** (Koidz.) Fernald.

We have just received a copy of Notulae Systematicae, vol. viii, fasc. 4–9 (1940), wherein is described (p. 111) and figured (p. 112) *Primula renifolia* Volgunov. This species is compared with *P. Meyeri* Rupr. (*P. amoena* var. *Meyeri* (Rupr.) Boiss.). Specimens in the Herbarium of the Inst. Bot. Ac. Sc. URSS are not available to us, but from the figure and the description this plant appears to bear a striking resemblance to a dwarf or poorly developed form of *P. megaseaefolia* Boiss.

REPORT OF THE ANNUAL CONFERENCE OF THE CRYPTOGAMIC SECTION, 1948.

By C. E. FOISTER, B.A., Ph.D.

(Read 19th May 1949.)

The Sixtieth Annual Conference of the Cryptogamic Section of the Society was held at Thornhill and district (Dumfriesshire) on 1st to 3rd October 1948, His Grace the Duke of Buccleuch kindly consenting to the forays being held on his property.

Scar Valley, Penpont, was visited on 1st October and a reasonably good collection of fungi was made, though the agarics were not so plentiful as was expected from the wet weather experienced in September. At the evening business meeting it was decided to have the 1949 autumn foray in the Dollar district, while an invitation was accepted to visit the plant pathology laboratories at Auchincruive, Ayr, in conjunction with a short spring foray in that district. Mr. D. M. Henderson was elected as assistant secretary.

Drumlanrig Castle policies (Tibbers and Newlands Woods) were visited on 2nd October, when members of the Dumfries and Galloway Natural History Society joined in the forays and again a good collection resulted, including a fair number of non-mycological finds. Morton Woods were visited on 3rd October, when a surprisingly good agaric collection was made. The collections were studied and displayed at the Morton Academy, Thornhill, where the Rector, Mr. Cowan, kindly provided every facility. Thanks are also due to Dr. Malcolm Wilson, Mr. J. A. Johnstone, and Dr. J. Grainger for their generous help in the identification of the specimens. Throughout the three days a very pleasant and profitable time was spent in reasonably good weather conditions. A total of twenty-five attended.

LIST OF CRYPTOGAMS COLLECTED.

FUNGI.

HYMENOMYCETES.

Amanita citrina (Schaeff.) Quél.; muscaria (L.) Fr.; rubescens (Pers.) Fr.
Amanitopsis fulva (Schaeff.) W. G. Smith
Anellaria separata (L.) Karst.
Armillaria mellea (Vahl.) Fr.; mucida (Schrad.) Fr.
Boletus badius Fr.; erythropus (Pers.) Quél.
Calocera cornea (Batsch) Fr.; viscosa (Pers.) Fr.
Cantharellus cibarius Fr.

Clavaria cinerea (Bull.) Fr.; cristata (Holmsk.) Fr.; dissipabilis Britzl.; fumosa (Pers.) Fr.; muscoides Fr.; rugosa (Bull.) Fr.

Clitocybe clavipes (Pers.) Fr.; fragans Sow.; infundibuliformis (Schaeff.) Fr.; metachroa (Fr.) Berk.; nebularis (Batsch) Fr.; odora (Bull.) Fr.; phyllophila Fr.; vibecina Fr.

Collybia butyracea (Bull.) Fr.; distorta Fr.; maculata (A. & S.) Fr.; platyphylla (Pers.) Fr.; radicata (Rehl.) Berk.; tuberosa (Bull.) Fr. on Russula nigricans (Bull.) Fr.

Coprinus micaceus (Bull.) Fr.

Cortinarius cinnamomeus (L.) Fr.; elatior Fr.; paleaceus (Weinm.) Fr.; torvus Fr.

Craterellus sinuosus Fr.

Crepidotus mollis (Schaeff.) Fr.

Dacryomyces deliquescens (Bull.) Duby

Dictyolus muscigenus (Bull.) Quél.

Entoloma rhodopolium Fr.

Flammula alnicola Fr.; carbonaria Fr.

Fomes annosus Fr.

Ganoderma applanatum (Pers.) Pat.

Hirneola auricula-judae (L.) Berk.

Hydnum repandum (L.) Fr.

Hygrophorus chlorophanus Fr.; coccineus (Schaeff.) Fr.; laetus (Pers.) Fr.; psittacinus (Schaeff.) Fr.; puniceus Fr.; unguinosus Fr.; virgineus (Wulf.) Fr.

Hypholoma hydrophilum (Bull.) Fr.; fasciculare (Huds.) Fr.; sublateritium (Schaeff.) Fr.; velutinum (Pers.) Fr.

Inocybe geophylla (Sow.) Fr.; var. lilacina Fr.

Laccaria laccata (Scop.) B. & Br.; var. amethystina (Vaill.) B. & Br.

Lactarius blennius Fr.; chrysorheus Fr.; piperatus (Scop.) Fr.; pyrogalus (Bull.) Fr.; quietus Fr.; subdulcis (Pers.) Fr.; turpis (Weinm.) Fr.; vellereus Fr.

Lepiota amianthina (Scop.) Fr.; carcharius (Pers.) Fr.; hacodes (Vitt.) Fr.

Marasmius androsaceus (L.) Fr.; hariolorum (DC.) Quél.; peronatus (Bolt.) Fr.

Mycena alcalina Fr.; corticola (Schum.) Fr.; flavo-alba Fr.; galericulata (Scop.) Fr.; polygramma (Bull.) Fr.; pura (Pers.) Fr.; sanguinolenta (A. & S.) Fr.; setosa (Sow.) Fr.; tenerrima Berk.; vitilis Fr.

Nyctalis asterophora Fr.; parasitica (Bull.) Fr.

Panaeolus campanulatus (L.) Fr.

Panus stipticus (Bull.) Fr.

Pholiota squarrosa (Mull.) Fr.

Phylacteria terrestris (Ehrh.) Big. & Guill.

Pleurotus ostreatus (Jacq.) Fr.

Pluteus cervinus (Schaeff.) Fr.

Polyporus betulinus (Bull.) Fr.; caesius (Schrad.) Fr.

Polystictus versicolor (L.) Fr.

Russula atropurpurea (Krombh.) Maire; cyanoxantha (Schaeff.) Fr.; emetica (Schaeff.) Fr.; fellea Fr.; lutea (Huds.) Fr.; nigricans (Bull.) Fr.; ochroleuca (Pers.) Fr.

Stereum hirsutum (Willd.) Fr.; rugosum (Pers.) Fr.; sanguinolentum (A. & S.) Fr.; spadiceum Fr.

Stropharia aeruginosa (Curt.) Fr.; semiglobata (Batsch) Fr.

Tremella foliacea (Pers.) Fr.

Tremellodon gelatinosum (Scop.) Fr.

Tricholoma columbetta Fr.; nudum (Bull.) Fr.; terreum (Schaeff.) Fr.; ustale Fr.

Tubaria furfuracea (Pers.) W. G. Smith

GASTEROMYCETES.

Crucibulum vulgare Tul.
Phallus impudicus (L.) Pers.
Lycoperdon perlatum Pers.; pyriforme (Schaeff.) Pers.
Scleroderma aurantium Pers.

UREDINALES.

Cumminsiella sanguinea (Peck) Arthur on Mahonia aquifolium (Pursh) Nutt.
Gymnosporangium juniperi Link on Sorbus aucuparia L.
Melampsora larici-caprearum Kleb. on Salix sp.
Melampsorella cerastii Schroet. on Stellaria graminea L.
Melampsoridium betulinum Kleb. on Betula pendula Roth.
Phragmidium disciflorum James on Rosa sp.
Puccinia acetosae Korn on Rumex acetosa L.; centaureae DC. on Centaurea nigra L.; chaerophylli Purt. on Anthriscus sylvestris (L.) Hoffm.; chrysosplenii Grev. on Chrysosplenium oppositifolium L.; circaeae Pers. on Circaea lutetiana L.; holcina Erikss. on Holcus mollis L.; lapsanae Fckl. on Lapsana communis L.; lemonnieriana Maire on Cirsium palustre (L.) Scop.; luzulae-maximae Diet. on Luzula sylvatica (Huds.) Gaud.; lychnidearum Link on Melandrium dioicum (L.) Coss & Germ. and Stellaria media (L.) Vill.; veronicae Schroet. on Veronica montana L.; winteriana Magnus on Phalaris arundinacea L.
Pucciniastrum circaeae Speg. on Circaea lutetiana L.; epilobii Otth. on Chamaenerion angustifolium (L.) Scop.
Thecopsora vacciniorum Karst. on Vaccinium myrtillus L.
Triphragmium ulmariae Wint. on Filipendula ulmaria (L.) Maxim.
Uromyces alchemillae Pers. on Alchemilla vulgaris sp. agg.; fabae de Bary on Vicia sepium L.; geranii Otth. & Wart. on Geranium sylvaticum L.

USTILAGINALES.

Entyloma microsporum (Unger) Schroet. on Ranunculus repens L.
Urocystis anemones (Pers.) Wint. on Ranunculus repens L.
Ustilago violacea (Pers.) Rous. on Melandrium dioicum Coss & Germ.

ASCOMYCETES.

Bulgaria inquinans (Pers.) Fr.
Chlorosplenium aeruginosum de Not.
Claviceps purpurea (Fr.) Tul. on Deschampsia caespitosa (L.) Beauv. and Dactylis glomerata L.
Cordiceps ophioglossoides (Ehrh.) Link on Elaphomyces variegatus Fr.
Coryne sarcoides (Jacq.) Tul.
Geopyxis cupularis (L.) Sacc.
Leotia lubrica (Scop.) Fr.
Nectria cinnabarina (Tode) Fr.
Phacidium ilicis Lib. on Ilex aquifolium L.
Phyllacora graminis (Pers.) Fuckel on Dactylis glomerata L.
Phyllactinia corylea (Pers.) Karst.
Rhopographus pteridis (Sow.) Rab. on Pteridium aquilinum (L.) Kuhn
Rhytisma acerinum Fr. on Acer pseudo-platanus L.
Sclerotinia curreyana (Berk.) Karst. on Juncus effusus L.

Stegia ilicis Fr. on Ilex aquilifolium L.
Uncinula aceris (DC.) Sacc. on Acer pseudo-platanus L.
Xylaria carpophila (Pers.) Fr. on beech mast; hypoxylon (L.) Grev.; polymorpha (Pers.) Grev.

PHYCOMYCETES.

Empusa muscae (Fr.) Cohn

IMPERFECTI.

Mastigosporium rubricosum (Dearn. & Barth.) Sprague on Dactylis glomerata L.
Pycnostysanus (Sporocybe) azalae (Peck) Sacc. on Rhododendron sp.

LICHENS.

Evernia furfuracea Mann.
Peltigera canina Willd.
Usnea barbata Web.

MOSSES.

Catharinea undulata W. & M.
Hypnum cupressiforme L.; cuspidatum L.
Mnium hornum L.; undulatum L.
Polytricum commune L.
Thuidium tamariscinum B. & S.

FERNS.

Asplenium trichomanes L.
Athyrium filix-femina (L.) Roth
Blechnum spicant (L.) Roth
Dryopteris dilatata (Hoffm.) A. Gray; filix-mas sp. agg.
Polypodium vulgare L.
Pteridium aquilinum (L.) Kuhn
Thelypteris oreopteris (Ehrh.) C. Chr.; phegopteris (L.) Slosson

THE SPORES OF LYCOPODIUM, PHYLLOGLOSSUM, SELAGINELLA AND ISOETES

AND THEIR VALUE IN THE STUDY OF MICROFOSSILS OF PALAEOZOIC AGE

BY

ELIZABETH M. KNOX, M.A., D.Sc.

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THE SPORES OF LYCOPODIUM, PHYLLOGLOSSUM, SELAGINELLA AND ISOETES, AND THEIR VALUE IN THE STUDY OF MICROFOSSILS OF PALAEOZOIC AGE. By ELIZABETH M. KNOX, M.A., D.Sc. (With Pls. VIII–XIX.)

INTRODUCTION.

The LYCOPODIINAE are a ubiquitous race of plants, its members being found in many different parts of the world from the tropics to the polar regions, and under a great variety of habitat conditions.

The families with living representatives afford ample evidence of antiquity, and their fossil relatives indicate the abundance of the group during Palaeozoic times. The coals of Carboniferous Age are to a large extent composed of the carbonised remains of these plants, and their spores are found in vast numbers in most coal-seams.

The study of fossil spores within the last twenty-five years has led to their being used as an aid in the correlation of coal-seams. Up to the present the classification of fossil spores has been an arbitrary one, but with the increasing use of spores as zonal indices in coalfield work, a more scientific system of nomenclature has been found necessary. A binomial system has been promulgated in America which in all probability will form the basis of future work on classification. Although a general review of the spores of modern Pteridophyta has already been published by the author (Knox, 1938), the lack of any comprehensive survey of the spore morphology of living species of Vascular Cryptogams has proved a considerable handicap in framing a classification of fossil spores. Accordingly the present study of the spores of modern species of LYCOPODIINAE has been undertaken with a view to gaining more exact knowledge of spore morphology in this large and important group, both generic and specific, in order to make possible an assessment of relative values for purposes of palaeobotanical taxonomy. The account is based upon a detailed study of the spores of Lycopodium, Phylloglossum, Selaginella and Isoetes, derived from as many species as it has been possible to examine.

The earliest mention of the family *Lycopodiaceae* was by Dodoneus in the sixteenth century. About 1585 he used the name Lycopodium and gave it to the plant which in all probability is now referred to as *Lycopodium Selago*. Subsequent to that date members of the family were variously designated as Selago, Selaginoides or Lycopodium. Dillenius in his "Historia Muscorum" (1741) made one of the earliest attempts at classification, and distinguished as distinct genera Selago, Selaginoides, Lycopodium and Lycopodiodes. It was not until the following century that homospory, heterospory, and the presence or absence of a ligule were recognised as of diagnostic value. That there were two kinds of spores in certain species of Selaginella was known to Dillenius, but the exact nature of the megaspores was in dispute for a long time. Not until Lindsay, in 1792, germinated the spores of *Lycopodium clavatum* was the function of the spores in Lycopodium recognised.

Kaulfuss (1824) mentions the tetrahedral nature of spores in his "Enumeratio Filicum", and describes many genera and species; he also appends an exhaustive bibliography with references going back as far as 1533. The earliest figures of spores are to be found in Hooker and Greville's "Icones Filicum" (1831), and further illustrations are given by Mohl (1833). Later, in 1854, Brackenridge figures a few of the species collected by the U.S. Exploratory Expedition to the Pacific Islands. The figures of these earlier writers all suffer from the same disadvantage in that they are so small as to be almost valueless. Spring's classic Monograph, published in 1842–1849, marks the beginning of the modern approach to classification. He recognised four genera: Lycopodium, Selaginella, Tmesipteris and Psilotum. Spring's work was followed by several systematic accounts, notably those of Luerssen (1879), Baker (1887), Pritzel (1901), Herter (1909) and Hirmer (1927). Baker, in "Handbook of Fern-Allies" (1887), separates the *Selaginellaceae* (including Isoetes) from the *Lycopodiaceae*, referring Psilotum and Tmesipteris to the latter family. Pritzel (Naturl. Pflanzenfam., 1901), on the other hand, divides the *Lycopodiales* into *Eligulatae* (including *Lycopodiaceae* and *Psilotaceae*) and *Ligulatae* (including *Selaginellaceae*, *Isoetaceae* and three fossil families), whereas Hirmer (1927) removes the living *Psilotaceae* from the *Lycopodiales* and places it in a separate order *Psilotales*. In *Lycopodiales* he includes *Lycopodiaceae*, *Selaginellaceae*, *Isoetaceae* and five fossil families. This latter arrangement is nearest to the modern one propounded by Eames (1936), who also places Psilotum and Tmesipteris in a separate order *Psilotales*, since, as he says "the group is so unlike other vascular plants that it must stand by itself in the order *Psilotales*, an order isolated from the other living orders. In taxonomic and morphologic treatments the family has often been grouped with the *Lycopodiaceae*; but it is evident that such a grouping is unnatural, for not only are the *Psilotaceae* leafless and rootless and their sporangia cauline and terminal, but the sperms are multiciliate and the antheridia superficial". Eames (*l.c.*) also raises Lycopodium and Selaginella to ordinal rank, pointing out that though "remarkable for their strong resemblances and their marked differences they are undoubtedly related but not closely". And he goes on to say: "It is generally believed that the differences are great enough to justify ordinal rank; the club mosses, therefore, form two small orders, *Lycopodiales* and *Selaginellales*, which stand more or less together, each containing a single family." Both Hirmer and Eames maintain a separate order *Psilophytales* for the fossil plants *Rhynia*, *Hornea* and their allies. The relationship of these fossils to the *Psilotaceae* is obscure but, according to Eames, "there can be little doubt but that the *Psilotaceae* represent surviving remnants of the ancient psilophytalean stock, retaining the major morphological features of the ancestral types. As such they are living examples of the oldest known vascular plants".

So far as is known to the present author no systematic account of the spores of the LYCOPODIINAE, with specific descriptions and figures, has been published, though, scattered through the literature, figures and descriptions are to be found. The present intention is to make as comprehensive a study of the microspores of the families *Lycopodiaceae*, *Selaginellaceae* and *Isoetaceae* as is possible, having regard to the availability of material for study.

LYCOPODIACEAE.

GENERAL CHARACTERS AND CLASSIFICATION.

In the family *Lycopodiaceae* the sporophytes are herbaceous with stems bearing small simple leaves. The fertile leaves are usually aggregated in definite cones and the sporangia are homosporous. The family is an ancient one, extending back to the Carboniferous Period, and at the present time represented by two living genera, Lycopodium and Phylloglossum, a monotypic genus known only from Australia and New Zealand.

In Baker's "Handbook of Fern-Allies" (1887) the genus Lycopodium is divided into four sub-genera:

Sub-genus I. SELAGO. Sporangia placed in the axils of unaltered leaves all down the stem. Leaves multifarious.

Sub-genus II. SUBSELAGO. Sporangia in indistinct terminal spikes. Leaves multifarious.

Sub-genus III. LEPIDOTIS. Sporangia aggregated into distinct terminal spikes. Leaves multifarious.

Sub-genus IV. DIPHASIUM. Sporangia collected into terminal spikes, with small bracts. Leaves distichous and dimorphous.

Pritzel (1901) recognised two sub-genera only, differing in general organisation of the sporophyte and in exospore morphology, viz.

Sub-genus I. UROSTACHYA. Species with branched or unbranched stems, erect or pendent; no adventitious roots along the stem; foliage leaves and sporophylls approximately the same size; *exospore pitted or granular.*

Sub-genus II. RHAPALOSTACHYA. Species with prostrate stems and upright branches; adventitious roots borne along the length of the prostrate portion of the creeping stem; sporophylls in well-defined strobili, and different from the foliage leaves; *exospore reticulate.*

Herter (1909), on the other hand, divides the genus into six sub-genera, of which UROSTACHYA (which he raises to generic rank in later papers) contains the largest number of species, and is the only sub-genus with which he has dealt systematically. This sub-genus, which is that of Pritzel (1901) with certain emendations, Herter (1909) divides into: (1) *Eurostachys*, with leaves and sporophylls alike; (2) *Heterostachys*, with strobili differentiated from vegetative parts.

The most recent classification, that of Walton and Alston (1938), is a simplification of Herter's, maintaining the six sub-genera of that author, but raising certain of Baker's groups to sub-generic rank. The arrangement of Walton and Alston is as follows:—

Sub-genus I. UROSTACHYS.

Section 1. *Selago.* Erect terrestrial species; leaves and sporophylls similar.

Section 2. *Sub-Selago.* Pendent epiphytes; leaves and sporophylls similar.

Section 3. *Phlegmaria.* Strobili strongly different from vegetative parts.

Sub-genus II. CLAVATOSTACHYS corresponds to Baker's group of *L. clavatum.*

Sub-genus III. COMPLANATOSTACHYS corresponds to Baker's sub-genus DIPHASIUM, with the addition of *L. casuarinoides*.

Sub-genus IV. CERNUOSTACHYS corresponds to Baker's group of *L. cernuum,* excluding *L. casuarinoides.*

Sub-genus V. INUNDATOSTACHYS corresponds to Baker's group of *L. inundatum.*

Sub-genus VI. LATERALOSTACHYS corresponds to Baker's group of *L. laterale,* and includes only two species, *L. diffusum* and *L. laterale.*

It has not been found practicable to employ any of the foregoing systems of classification in the account of the spores which follows. The scheme here adopted is one in which the species are arranged in groups according to spore characters alone, since the purpose of this investigation is to provide a comparative account of spore morphology and not a taxonomic treatment of the genus.

Of the 94 species of Lycopodium enumerated by Baker, the author has been able to obtain for examination 91 and a number of varieties. During recent years many previously named varieties have been accorded specific rank, bringing the number of species in Lycopodium to over 300. It has been considered unnecessary to examine all the varietal forms, and the species enumerated by Baker (1887) have been regarded as adequate for purposes of the present work. Where varietal forms, now raised to specific rank, have been examined, the spores have been found to be essentially similar to those of the species from which they have been segregated.

METHOD OF TREATMENT.

A uniform method of treatment and examination has been maintained throughout. The strobili were boiled for one minute in 10 per cent. KOH, washed in distilled water and dehydrated in absolute alcohol. Two mounts were made from each sample, one in glycerine jelly stained with Malachite Green, and the other in Euparal-Vert. On each slide not fewer than 10 spores were measured and the average of the measurements recorded.

As already stated, existing taxonomic arrangements for the genera with which this study is concerned cannot be adopted, since the investigation deals primarily with the comparative morphology of the spore; and in the case of Selaginella and Isoetes only the microspores are dealt with. In the construction of keys, based on spore morphology, it has been necessary to make use of minute characters, and all descriptions are drawn up from spores examined under a magnification of 350 diameters.

Key to the Genera Lycopodium, Phylloglossum, Selaginella and Isoetes.

A. Spores ovoid in outline, bilateral	*Isoetes*
AA. Spores spherical to triangular in outline, tetrahedral.	
B. Exospore without ornamentation	*Selaginella*
BB. Exospore with ornamentation.	
C. Exospore bearing emergent processes	*Selaginella*
CC. Exospore not bearing emergent processes.	
D. Exospore pitted	*Lycopodium*
DD. Exospore ridged or reticulate	*Lycopodium* *Phylloglossum*

GENUS I. LYCOPODIUM.

Key to Groups in Lycopodium.

A. Spore ornamentation reticulate or with anastomosing ridges	IV. Group CLAVATUM
AA. Spore ornamentation not as above.	
B. Spore ornamentation pitted.	
C. Pits round, distinct.	
D. Sides of spore more or less concave, angles truncate	I. Group SELAGO
DD. Sides of spore straight or convex	II. Group PHLEGMARIA
CC. Pits coalescent or elongate	III. Group VERTICILLATUM
BB. Spore ornamentation spinose	*L. densum*

Group I. GROUP OF L. SELAGO.

Spores measuring 25–45 μ. Tetrahedral with sub-triangular outline. Sides straight or concave and angles truncate. Exospore ornamented with shallow pits averaging 2 μ in diameter, spaced 2–5 μ apart.

Key to the Species.

A. Spore diameter exceeding 35 μ.	
B. Pits 2–3 μ across	*L. Selago*, fig. 1
BB. ,, 1 μ ,,	*L. fontinaloides*, fig. 2
AA. Spore diameter less than 35 μ.	
B. Angles truncate.	
C. Pits 2–3 μ across	*L. serratum*, fig. 3
CC. ,, 1–2 μ ,,	*L. miniatum*, fig. 4
BB. Angles obtuse	*L. ceylanicum*, fig. 5 *L. lucidulum*, fig. 6

L. ceylanicum Spring (fig. 5).

Tetrahedral, sub-triangular, 30–35 μ. Wall 3 μ in thickness. Sides of spore slightly concave and angles obtuse, not markedly truncate. Exospore pitted; pits small, 1–2 μ, and spaced 2–3 μ apart. Spore margin irregular and undulating, with indication of pits.

The spores are not mentioned by Spring (1842, p. 38), though he remarks upon the affinity of this species with *L. lucidulum* (fig. 6). Baker says the species is intermediate between *L. lucidulum* and *L. Selago* (fig. 1), and this view is corroborated by the similarity in spore structure of the three species.

L. fontinaloides Spring (fig. 2).

Tetrahedral, sub-triangular, 35–40 μ. Wall 3–4 μ in thickness. Tetrad scar extending to the margin. Corners of the spore are angular, and the sides straight or slightly concave. Exospore finely punctate; the minute pits, 1 μ across, are regularly disposed, about 2–3 μ apart, on all faces.

The spores of this species are mentioned by Spring (1842, p. 49).

L. lucidulum Michx. (fig. 6).

Tetrahedral, sub-triangular, 30–40 μ. Wall 2–3 μ in thickness. Tetrad scar extending to the margin. Sides of spore slightly concave, angles obtuse. Exospore pitted; pits small, 1–2 μ, spaced 2–3 μ apart on the ab-apical side, becoming less distinct on the apical face. Margin faintly sinuous.

The spores are described and figured by Wilson (1934, p. 18, Pl. 275).

L. miniatum Spring (fig. 4).

Tetrahedral, sub-triangular, 30–40 μ. Wall 3 μ in thickness. Tetrad scar extending almost to the margin. Sides of spore straight or slightly concave, angles truncate. Exospore pitted; pits small, 1–2 μ, spaced 3–5 μ apart. On the apical surface the pitting is less well marked, and the pits are frequently absent from the concave sides.

The spores of this species are mentioned by Spring (1842, p. 28). He remarks that this species "rapproche beaucoup" *L. reflexum* (fig. 29) of S. America. This similarity is not seen in the spore structure, where the resemblance is with *L. Selago* (fig. 1). Herter (1909) classes *L. miniatum* with *L. Selago*, thus recognising their affinity.

L. Selago L. (figs. 1 *a* and *b*).

Tetrahedral, sub-triangular, 35–45 μ. Wall 2–3 μ in thickness. Tetrad scar 2/3 radius. Sides of spore slightly concave, angles truncate. Exospore pitted; pits distinct, 2 μ in diameter, regularly disposed on the ab-apical surface, about 3 μ apart, becoming irregular or absent round the apical crest.

Mohl (1833) mentions the spores and gives a minute and inadequate figure. Luerssen (1889) describes the spores as having an irregular network, most pronounced on the rounded face; Bruchmann (1910) states they are frequently pitted, 40 μ in diameter, and figures them with thickened corners. Wilson (1934, p. 275) also describes and figures the spores. Baker (1887) considers *L. suberectum* Lowe, *L. Haleakalae* Brack. and *L. erubescens* Brack. to be forms of *Selago*. Brackenridge (1854) gives no description of the last two forms and only very inadequate figures; descriptions and figures of both are given by Selling (1946, p. 11) and show affinities with *Selago*. Wilson (1934, p. 18, Pl. 275) groups *L. Selago* together with *L. lucidulum* (fig. 6) as primitive species; both exhibit characteristic concave sides and papillation.

L. serratum Thunb. (figs. 3 *a* and *b*).

Tetrahedral, sub-triangular, 25–35 μ. Wall 2 μ in thickness. Tetrad scar extending almost to the margin. Sides of spore slightly concave, angles truncate. Exospore with shallow pits 2–3 μ across and 3 μ apart on the ab-apical surface; the apical side is almost smooth.

The earliest description of the spores of this species is by Hooker and Greville (1831, tab. 37); their figure with reticulate ornamentation is misleading. Spring (1842, p. 39) mentions the spores under *L. sulcinervium*. Selling (1946, p. 13) describes and figures the spores.

Group II. Group of L. Phlegmaria.

Spores measuring 25–60 μ in diameter. Tetrahedral, with sub-triangular outline; sides of spores almost straight to slightly convex. Exospore pitted. Pits small, not exceeding 3 μ across, variously spaced from 2 to 10 μ apart.

The spores within this large group have few features by which they can be readily separated from one another, and many are almost indistinguishable from each other. The key attempts no more than to bring together those species which have similar spore characters.

Key to the Species.

A. Pits rather dense and closely arranged, 2–3 μ apart.
  B. Spore diameter greater than 40 μ . . *L. funiforme*
    L. robustum, fig. 8
    L. Sieboldi, fig. 7
    L. strictum

BB. Spore diameter less than 40 μ.
C. Spore diameter 30–40 μ . . . . *L. aqualupianum*, fig. 9
L. callitrichaefolium, fig. 10
L. carinatum, fig. 11
L. casuarinoides, fig. 12
L. cryptomerinum, fig. 13
L. Dalhousianum, fig. 14
L. erythraeum, fig. 15
L. filiforme
L. Hamiltonii, fig. 16
L. mollicomum, fig. 17
L. myrsinites, fig. 18
L. Phlegmaria, fig. 19
L. sarmentosum, fig. 20
CC. Spore diameter 25–30 μ . . . . *L. dichotomum*, fig. 21
L. phlegmarioides

AA. Pits arranged more than 3 μ apart.
B. Pits widely spaced 5–8 μ apart.
C. Spore diameter greater than 40 μ . . *L. firmum*, fig. 22
L. Hartwegianum
L. Lindeni, fig. 23
L. megastachyum, fig. 24
L. Saururus, fig. 25
L. Trencilla
CC. Spore diameter 35–40 μ . . . . *L. compactum*, fig. 26
L. Jamesoni, fig. 27
L. obtusifolium, fig. 28
L. reflexum, fig. 29
L. tetragonum, fig. 30
BB. Pits spaced 3–5 μ apart.
C. Spore diameter greater than 40 μ . . *L. affine*, fig. 31
L. attenuatum
L. echinatum, fig. 32
L. gnidioides, fig. 33
L. myrtuosum, fig. 34
L. rigidum
L. rufescens, fig. 35
L. setaceum, fig. 36
L. subulatum, fig. 37
CC. Spore diameter 30–40 μ . . . . *L. apiculatum*
L. Billardieri, fig. 38
L. cancellatum, fig. 39
L. coralium
L. dacrydioides
L. insulare, fig. 40
L. linifolium
L. nummularifolium, fig. 41
L. ophioglossoides
L. Pearcei, fig. 42
L. Pecten
L. pinifolium, fig. 43
L. squarrosum
L. varium
L. Vrieseanum

L. affine Hook. & Grev. (fig. 31).

Tetrahedral, sub-triangular, 45–50 μ. Walls 5 μ in thickness. Tetrad scar extending almost to the margin. Sides of spore convex. Exospore pitted; pits small, 1 μ, set 3–5 μ apart.

Spring (1842, p. 21) discusses the affinities of the species but does not mention the spores.

L. apiculatum Spring

Tetrahedral, sub-triangular, 35 μ. Wall thin. Tetrad scar extending to the margin. Sides of spore straight to convex. Exospore pitted; pits small, 1μ deep, and regularly spaced 3μ apart.

No mention of the spores of this species has been found in the literature. Baker (1887) states it is nearly allied to *L. Phlegmaria* (fig. 19); the spores of the two species are similar.

L. aqualupianum Spring (fig. 9).

Tetrahedral, sub-triangular, 30–35 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, regular, and spaced 2–3 μ apart.

L. attenuatum Spring

Tetrahedral, sub-triangular, 40 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Sides of spore almost straight or slightly convex. Exospore pitted; pits small, 1 μ, spaced 3–5 μ apart.

The spores of this species are mentioned by Spring (1849, p. 8); he remarks on the close affinity to *L. erythraeum* (fig. 15).

L. Billardieri Spring (fig. 38).

Tetrahedral, sub-triangular, 35–40 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Sides of spore slightly convex. Exospore pitted; pits 2 μ across and varying from 3 to 7 μ apart.

No description of the spores of this species has been found in the literature.

L. callitrichaefolium Mett. (fig. 10).

Tetrahedral, sub-triangular, 35–40 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Sides of spore convex. Exospore pitted; pits small, deep, and regularly arranged 2–3 μ apart.

No description of the spores of this species has been found in the literature. Both Baker (1887) and Herter (1909) relate the species to *L. Phlegmaria* (fig. 19), and the spore sculpturing is similar in the two species.

L. cancellatum Spring (fig. 39).

Tetrahedral, sub-triangular, 30–35 μ. Wall 2–3 μ in thickness. Tetrad scar extending to the margin. Sides of spore straight. Exospore pitted; pits small, 1–2 μ across, regularly arranged 3–5 μ apart.

L. carinatum Desv. (fig. 11).

Tetrahedral, sub-triangular, 35–40 μ. Wall 2 μ in thickness. Tetrad scar extending almost to the margin. Sides of spore straight and angles rounded. Exospore pitted; pits small, 1 μ, regularly spaced 2–4 μ apart.

The spores of this species are mentioned by Hooker and Greville (1831, tab. 181).

L. casuarinoides Spring (fig. 12).

Tetrahedral, sub-triangular, 30–40 μ. Wall thin. Tetrad scar extending to the margin. Sides of spore slightly convex. Exospore pitted; pits small, 1 μ, spaced 2–3 μ apart.

The spores of this species are mentioned by Spring (1849, p. 45).

L. compactum Hook. (fig. 26).

Tetrahedral, sub-triangular, 35–45 μ. Wall 2–3 μ in thickness. Tetrad scar extending to the margin. Sides of spore convex. Exospore pitted; pits small, 1 μ, spaced 5–8 μ apart on all surfaces.

The spores of this species are mentioned by Spring (1842, p. 9).

L. coralium Spring

Tetrahedral, sub-triangular, 30–35 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, regularly spaced 3 μ apart. The spores of this species are almost indistinguishable from those of *L. pinifolium* (fig. 43).

L. cryptomerinum Maxim. (fig. 13).

Tetrahedral, sub-triangular, 30–40 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits 1–2 μ across and regularly spaced 2–3 μ apart.

L. dacrydioides Baker

Tetrahedral, sub-triangular, 35–40 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, and spaced 3–5 μ apart. Similar to *L. gnidioides* (fig. 33).

L. Dalhousianum Spring (fig. 14).

Tetrahedral, sub-triangular, 35 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Sides of spore slightly convex. Exospore pitted; pits small, 1 μ, regularly arranged and closely set 2 μ apart.

The spores of this species are mentioned by Spring (1849, p. 25).

L. dichotomum Jacq. (fig. 21).

Tetrahedral, sub-triangular, 25–30 μ. Wall thin. Tetrad scar extending almost to the margin. Exospore pitted; pits small, 1 μ, shallow and closely spaced 2 μ apart.

L. echinatum Spring (fig. 32).

Tetrahedral, sub-triangular, 55–60 μ. Wall 5 μ in thickness. Tetrad scar extending to the margin. Sides of spore convex. Exospore pitted; pits small, 1 μ, and spaced 3–5 μ apart.

The spores of this species are mentioned by Spring (1849, p. 24).

L. erythraeum Spring (fig. 15).

Tetrahedral, sub-triangular, 30–40 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 2 μ, and 2–3 μ apart.

The spores of this species are mentioned by Spring (1849, p. 7).

L. filiforme Roxb.

Tetrahedral, sub-triangular, 30–35 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits 2 μ across and regularly spaced 2–3 μ apart.

No mention of the spores of this species has been found in the literature. Baker remarks that this species is scarcely more than a slender form of *L. Phlegmaria* (fig. 19), and the spores of the two are almost indistinguishable from one another.

L. firmum Mett. (fig. 22).

Tetrahedral, sub-triangular, 40–50 μ. Wall 5–6 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits minute and spaced 5 μ apart.

L. funiforme Chamisso

Tetrahedral, sub-triangular, 40–45 μ. Wall thin. Tetrad scar extending to the margin. Exospore pitted; pits 2–3 μ across on the ab-apical side, closely spaced, tending to give a reticulate appearance; the apical surface is smooth. The spores of this species are almost indistinguishable from those of *L. Sieboldi* (fig. 7).

L. gnidioides L. (fig. 33).

Tetrahedral, sub-triangular, 40–45 μ. Wall 2 μ in thickness. Tetrad scar extending almost to the margin. Exospore pitted; pits small, 1 μ, and regularly spaced 3–4 μ apart.

The spores of this species are mentioned by Hooker and Greville (1831, tab. 50) with a small inadequate figure.

L. Hamiltonii Spring (fig. 16).

Tetrahedral, sub-triangular, 30 μ. Wall thin. Tetrad scar extending to the margin. Sides of spore convex, angles rounded. Exospore pitted; pits 2 μ across and spaced 2–3 μ apart, giving a superficial reticulate appearance.

The spores of this species are mentioned by Hooker and Greville

(1831, tab. 233) under the specific name of *L. aloifolium* Wall. and by Spring (1849, p. 16).

L. Hartwegianum Spring

Tetrahedral, sub-triangular, 35–45 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Sides of spore almost straight. Exospore pitted; pits small, 1 μ, and spaced 5–7 μ apart.

The spores of this species are mentioned by Spring (1849, p. 14); they are similar in ornamentation to *L. tetragonum* (fig. 30).

L. insulare Carm. (fig. 40).

Tetrahedral, sub-triangular, 35–40 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Sides of spore almost straight. Exospore pitted; pits small, 1 μ, regularly spaced 3–4 μ apart.

Baker remarks that this species may be an extreme form of *L. Saururus* (fig. 25); the spores of both species are very similar.

L. Jamesoni Baker (fig. 27).

Tetrahedral, sub-triangular, 35–40 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Sides of spore almost straight. Exospore pitted; pits small, 1 μ, regularly spaced 5–6 μ apart.

L. Lindeni Spring (fig. 23).

Tetrahedral, sub-triangular, 40–50 μ. Wall 3–4 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits minute, regularly arranged, 5–8 μ apart.

The spores of this species are mentioned by Spring (1849, p. 27).

L. linifolium L.

Tetrahedral, sub-triangular, 35–40 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ across, and spaced 3–5 μ apart.

The spores of this species are mentioned by Spring (1842, p. 31); they are similar to *L. insulare* (fig. 40).

L. megastachyum Baker (fig. 24).

Tetrahedral, sub-triangular, 40–45 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, and irregularly spaced, varying from 3–10 μ apart. The surface of the spore appears rugose and the margin minutely sinuous.

L. mollicomum Mart. (fig. 17).

Tetrahedral, sub-triangular, 35 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Sides of spore slightly convex. Exospore pitted; pits 2 μ across, regularly spaced 2–3 μ apart.

L. myrsinites Lam. (fig. 18).

Tetrahedral, sub-triangular, 35 μ. Wall thin. Tetrad scar extending to the margin. Sides of spore convex. Exospore pitted; pits 2 μ across, regularly spaced 2 μ apart.

The spores of this species are mentioned by Spring (1842, p. 29).

L. myrtuosum Spring (fig. 34).

Tetrahedral, sub-triangular, 40–55 μ. Wall 4–5 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits minute, and spaced 3–5 μ apart.

The spores of this species are mentioned by Spring (1849, p. 10).

L. nummularifolium Blume (fig. 41).

Tetrahedral, sub-triangular, 35–40 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Sides of spore almost straight. Exospore pitted; pits small, 1–2 μ across, regularly spaced 3–4 μ apart.

The spores of this species are described by Hooker and Greville (1831, tab. 212).

L. obtusifolium Sw. (fig. 28).

Tetrahedral, sub-triangular, 25–40 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Sides of spore almost straight. Exospore pitted; pits minute, and spaced 3–8 μ apart.

L. ophioglossoides Lam.

Tetrahedral, sub-triangular, 35–40 μ. Wall 3–4 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1–2 μ, and regularly spaced 3–5 μ apart.

L. Pearcei Baker (figs. 42 *a* and *b*).

Tetrahedral, sub-triangular, 30–35 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, and regularly spaced 3–5 μ apart on the ab-apical side; round the apical crest the pits are more scattered.

L. Pecten Baker

Tetrahedral, sub-triangular, 35–45 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, and regularly spaced 3–5 μ apart.

L. Phlegmaria L. (figs. 19 *a* and *b*).

Tetrahedral, sub-triangular, 30–40 μ. Wall less than 2 μ in thickness. Tetrad scar extending to the margin. Sides of spore convex. Exospore pitted; pits small, 2 μ, regular and spaced 2–3 μ apart on the ab-apical surface; round the apical crest the pits are absent.

The spores of this species or its many varieties have been described by several authors. The earliest mention is by Spring (1842, p. 63); Lüstner (1898, p. 11) describes the spores of the type *Phlegmaria* as "tüpfelsporen". They are figured by Pritzel (1901, fig. 371) showing the pitted exospore. Robinson (1914) discusses the species and its several varieties; one of these, *L. Mannii* (Hillebr.) Skottsb., raised to specific rank by Skottsberg (1942, p. 132), is figured and described by Selling (1946, p. 16). The spores are similar to those of *L. Phlegmaria.*

L. phlegmarioides Gaudich.

Tetrahedral, sub-triangular, 25–30 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, regularly spaced 2 μ apart.

L. pinifolium Blume (fig. 43).

Tetrahedral, sub-triangular, 30–35 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, and spaced 3 μ apart.

The spores of this species are mentioned by Spring (1842, p. 58).

L. reflexum Lam. (fig. 29).

Tetrahedral, sub-triangular, 35–45 μ. Wall 4 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits minute and spaced 4 μ apart.

L. rigidum Gmel.

Tetrahedral, sub-triangular, 40–45 μ. Wall 4 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, spaced 3–4 μ apart.

Spring (1842, p. 25) and Baker (1887) both indicate that this species is very near to *L. reflexum* (fig. 29), and in both species the spore structure is closely similar.

L. robustum Klotzsch (fig. 8).

Tetrahedral, sub-triangular, 40–45 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits 2 μ across and spaced 2–3 μ apart.

L. rufescens Hook. (fig. 35).

Tetrahedral, sub-triangular, 40–45 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits minute and regularly spaced 3–5 μ apart.

L. sarmentosum Spring (fig. 20).

Tetrahedral, sub-triangular, 35–40 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1–2 μ across and spaced 2–3 μ apart, giving the appearance of a fine-meshed reticulum.

The spores of this species are mentioned by Spring (1849, p. 13).

L. Saururus Lam. (fig. 25).

Tetrahedral, sub-triangular, 40–45 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, spaced 5–8 μ apart.

The spores of this species are described by Hooker and Greville (1831, tab. 224) under *L. crassum*; they give a minute figure showing a tri-radiate mark but no ornamentation.

L. setaceum Hamilt. (fig. 36).

Tetrahedral, sub-triangular, 35–45 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, and regularly spaced 4 μ apart. The pitting is most pronounced on the ab-apical side, becoming indistinct round the apical crest.

The spores of this species are described by Hooker and Greville (1831, tab. 49); they give minute figures of spores and tetrads. Spring (1842, p. 43) also mentions the spores.

L. Sieboldi Miquel (fig. 7).

Tetrahedral, sub-triangular, 35–45 μ. Wall thin. Tetrad scar extending to the margin. Exospore pitted; pits 2–3 μ across and closely spaced 2 μ apart, giving a finely reticulate appearance to the ab-apical surface. The apical side is almost without ornamentation.

L. squarrosum Forst.

Tetrahedral, sub-triangular, 35–40 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, regularly spaced 3–5 μ apart.

The spores of this species are described and figured by Hooker and Greville (1831, tab. 185) under the name *L. Hookeri*; they are also mentioned by Spring (1842, p. 53).

L. strictum Baker

Tetrahedral, sub-triangular, 40–45 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, spaced 2–3 μ apart. Similar to *L. robustum* (fig. 8).

L. subulatum Desv. (fig. 37).

Tetrahedral, sub-triangular, 40–45 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Sides of spore convex. Exospore pitted; pits small, 1 μ, and spaced 5 μ apart.

L. tetragonum Hook. & Grev. (fig. 30).

Tetrahedral, sub-triangular, 35–40 μ. Wall 3 μ in thickness.

Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, spaced 5–8 μ apart.

The spores of this species are described by Hooker and Greville (1831, tab. 109) and by Spring (1849, p. 12).

L. Trencilla Sodiro

Tetrahedral, sub-triangular, 40 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ. deep and spaced 5–8 μ apart. The spores resemble closely those of *L. tetragonum* (fig. 30).

L. varium R. Br.

Tetrahedral, sub-triangular, 40–45 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ. deep and spaced 3–5 μ apart. The spore margin is slightly indented, due to the deep pitting.

The spores of this species are described by Hooker and Greville (1831, tab. 112); they are similar to those of *L. gnidioides* (fig. 33).

L. Vrieseanum Spring

Tetrahedral, sub-triangular, 35 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 1 μ, deep and regularly spaced 3 μ apart.

The spores of this species are mentioned by Spring (1849, p. 33); they are similar to *L. callitrichaefolium* (fig. 10).

Group III. GROUP OF L. VERTICILLATUM.

Spores measuring 30–45 μ. Tetrahedral, sub-triangular in outline with slightly convex sides. Exospore rugose and irregularly pitted. The pits tend to coalesce and form channels, separated by short, uneven ridges.

Key to the Species.

A. Channels confined to the equatorial margin .	*L. taxifolium*, fig. 44
AA. Channels on all surfaces.	
B. Channels pronounced.	
C. Spore diameter 35 μ	*L. verticillatum*, fig. 45
CC. ,, ,, 30 μ	*L. polytrichoides*, fig. 46
BB. Small pits between channels.	
C. Spore diameter 40–45 μ	*L. rubrum*, fig. 47
CC. ,, ,, 35–40 μ	*L. xiphophyllum*, fig. 48

L. polytrichoides Kaulf. (fig. 46).

Tetrahedral, sub-triangular to spherical, 30 μ. Wall 1–2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits shallow and close together, sometimes coalescent, forming short channels.

The spores of this species are described by Kaulfuss (1824, p. 6); Spring (1849, p. 33) remarks that this "species should be placed with *L. verticillatum* (fig. 45), with which it is liable to be confounded", and it is noteworthy that the spores can be placed together in the same group. A description and figure are given by Selling (1946, p. 14), who states that the sculpturing recalls the "irregular reticulum of *L. cernum*"; the resemblance does not seem to be very close.

L. rubrum Chamisso (fig. 47).

Tetrahedral, sub-triangular, 40–45 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits 2 μ across, coalescing to form short channels, giving the surface a rugose appearance.

The spores of this species are mentioned by Spring (1849, p. 28).

L. taxifolium Sw. (fig. 44).

Tetrahedral, sub-triangular, 40–45 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits small, 2 μ across, crowded; towards the equator they tend to coalesce, forming short grooves, which are a characteristic feature of the spores when seen in optical section.

L. verticillatum L. (fig. 45).

Tetrahedral, sub-triangular, 35 μ. Wall 2 μ in thickness. Tetrad scar extending to the margin. Exospore pitted; pits shallow, forming irregular short channels between small ridges.

The spores of this species are mentioned by Spring (1842, p. 46).

L. xiphophyllum Baker (fig. 48).

Tetrahedral, sub-triangular, 35–40 μ. Wall thin. Tetrad scar extending to the margin. Exospore pitted; pits irregular, about 2 μ across, sometimes coalescing to form elongate channels and giving the superficial appearance of a reticulum.

Group IV. Group of L. clavatum.

Spores measuring 25–65 μ. Sub-triangular to spherical in outline. The exospore is variously ornamented with ridges, which either unite to form a reticulum with alveoli of 5–15 μ in diameter, or remain as irregular broken ridges.

Key to the Species.

A. Exospore having a regular mesh structure on the ab-apical hemisphere.
  B. Mesh large, averaging 10 μ in diameter.
    C. Lamellae projecting from the margin about 5 μ.

D. Spore diameter 30–35 μ . . .	*L. diaphanum*, fig. 49
DD. ,, ,, 35–45 μ.	
E. Apical crest smooth . . .	*L. contiguum*, fig. 50
	L. Wightianum, fig. 51
EE. ,, ,, ridged	*L. vestitum*, fig. 53
CC. Lamellae low, not projecting from the margin more than 2 μ.	
D. Membranous fringe at the equator .	*L. volubile*, fig. 54
DD. No membranous fringe at the equator. .	
E. Apical crest smooth.	
F. Mesh 7–15 μ	*L. annotinum*, fig. 55
FF. ,, 5–10 μ	*L. scariosum*, fig. 52
EE. Apical crest not smooth.	
F. Apical crest channeled.	
G. Channels deep	*L. laterale*, fig. 56
GG. ,, fine	*L. ramulosum*, fig. 58
FF. Apical surface granular or reticulate.	
G. Granular	*L. magellanicum*, fig. 57
GG. Reticulate	*L. Sprucei*, fig. 59
BB. Mesh averaging less than 10 μ in diameter.	
C. Lamellae projecting from the margin 3–5 μ.	
D. Apical side with broken ridges . .	*L. clavatum*, fig. 61
DD. ,, ,, ,, smooth crest.	
E. Tetrad scar 2/3 radius . . .	*L. alpinum*, fig. 60
EE. ,, ,, extending to margin.	
F. Mesh 4–5 μ	*L. paniculatum*, fig. 62
FF. ,, 7 μ	*L. complanatum*, fig. 63
CC. Lamellae not projecting from surface.	
D. Tetrad scar in a furrow, surrounded by a clear area.	
E. Spore diameter 50–55 μ . . .	*L. adpressum*, fig. 64
EE. ,, ,, 25–30 μ . . .	*L. cernuum*, fig. 65
DD. Tetrad scar not in a furrow.	
E. Apical crest smooth.	
F. Spore diameter 40–50 μ . . .	*L. phyllanthum*, fig. 66
FF. ,, ,, 35–40 μ.	
G. Mesh 4–5 μ deep . . .	*Phylloglossum Drummondii*, fig. 67
GG. ,, 5–7 μ shallow . . .	*L. spurium*, fig. 68
EE. Apical crest with delicate mesh . .	*L. obscurum*, fig. 69
AA. Exospore with irregular ridges on the ab-apical hemisphere.	
B. Ab-apical surface with a broken mesh.	
C. Tetrad scar in a furrow.	
D. Apical side papillate	*L. Drummondii*, fig. 70
DD. ,, ,, with broken mesh . .	*L. inundatum*, fig. 71
CC. Tetrad scar not in a furrow . . .	*L. fastigiatum*, fig. 72
BB. Ab-apical surface irregularly ridged.	
C. Ridges anastomose	*L. carolinianum*, fig. 74
CC. ,, do not anastomose . . .	*L. diffusum*, fig. 73

L. adpressum Champ. (figs. 64 *a* and *b*).

Tetrahedral, almost spherical, 50–55 μ. Wall 5 μ in thickness. Tetrad scar 2/3 radius, surrounded by a clear unornamented area. Exospore with an irregular reticulate structure on the ab-apical side; the apical surface is papillate, with papillae extending to the clear area.

The spores of this species are described and figured by Wilson (1934, p. 18, Pl. 276) under the synonym *L. alopecuroides*.

L. alpinum L. (figs. 60 *a* and *b*).

Tetrahedral, almost spherical, 35 μ. Wall thin. Tetrad scar 2/3 radius. Exospore regularly reticulate on the ab-apical side; mesh 5–8 μ, with thin lamellae, projecting at the margin about 4 μ. Surrounding the apical crest ornamentation is absent, but towards the periphery a series of irregular ridges extending inwards for a distance of 15 μ are united at the edge by bars of the reticulum.

This species was first mentioned by Mohl (1833) as having reticulate spores. Spring (1842, p. 104) regards it as a varietal form of *L. complanatum* (fig. 63), as does Luerssen (1889), who describes the spores as similar in both species. The spores are described by Wilson (1934, p. 16) and Erdtman (1943, p. 148).

L. annotinum L. (figs. 55 *a* and *b*).

Tetrahedral, almost spherical, 35–40 μ. Wall thin. Tetrad scar extending to the margin. Exospore reticulate; mesh 7–15 μ across, with thin lamellae, on the ab-apical side; on the apical surface ornamentation is marginal, with a few irregular ridges extending about 10 μ inwards.

The spores of this species are described by several authors, all of whom remark on the reticulate exospore. The early writers Mohl (1833) and Luerssen (1889) give only short descriptions; illustrations are given by Bruchmann (1910), Wilson (1934, p. 19, Pl. 275) and Erdtman (1943, p. 148).

L. carolinianum L. (figs. 74 *a* and *b*).

Tetrahedral, almost spherical, 40–50 μ. Wall thin. Tetrad scar extending to the margin, situated in a furrow bounded by irregular thickenings. Exospore sculptured with irregular sinuous ridges, sometimes giving a sub-reticulate appearance.

The spores of this species are mentioned by Spring (1842, p. 98). Wilson (1934, p. 18, Pl. 276) describes and figures the spores; he also discusses the affinities of the species.

L. cernuum L. (figs. 65 *a* and *b*).

Tetrahedral, sub-triangular to spherical, 25 μ. Wall 2–3 μ in thickness. Tetrad scar situated in a furrow, surrounded by a definite margin. Exospore reticulate on the ab-apical side, mesh 5 μ. On the apical surface the ornamentation is uneven, rugose, but not reticulate.

This species of Lycopodium is common to many parts of the world and is mentioned frequently in literature; the spores are described by Hillebrand (1888) and Lüstner (1898), and later by Wilson (1934,

p. 19, Pl. 275), who gives a detailed account with figures; Selling (1946, p. 16) also describes and illustrates the spores.

L. clavatum L. (figs. 61 *a* and *b*).

Tetrahedral, almost spherical, 30 μ. Wall thin. Tetrad scar extending to the margin. Exospore reticulate; mesh 4–7 μ, lamellae thin and projecting at the periphery 3 μ. On the apical surface the reticulation is broken and irregular.

The spores of this species have been frequently referred to and figured. Mohl (1833) draws attention to the reticulate ornamentation; Hooker and Greville (1831, tab. 113), under the name *L. heterophyllum*, give a figure showing the reticulate structure; Luerssen (1889, fig. 222) and Lüstner (1898) describe and figure the spores, and both Wilson (1934, p. 19, Pl. 277) and Erdtman (1943, p. 148) give a detailed account.

L. complanatum L. (figs. 63 *a* and *b*).

Tetrahedral, sub-triangular, 30 μ. Wall thin. Tetrad scar extending to the margin. Exospore reticulate on the ab-apical side; mesh 4–7 μ, alveoli deep and lamellae projecting at the periphery about 3 μ. The apical crest is smooth and without ornamentation, but towards the equator anastomosing ridges extend inwards for a distance of 15 μ.

The spores of this species have been more often described than almost any other member of the genus. Among the earlier authors, Mohl (1833) and Druce (1882, p. 321) give small diagrams showing reticulation on the wall. Luerssen (1889) describes the spores as similar to those of *L. clavatum* (fig. 61) but with smaller and more regular reticulum, becoming indistinct or absent round the apical crest. Hegi (1936) gives a figure similar to that of Luerssen. Erdtman (1943, p. 148) describes and figures the spores, as does Wilson (1934, p. 19, Pl. 277), who also discusses the systematic position of related species, some of which he considers to be ecologically conditioned.

L. contiguum Klotzsch (figs. 50 *a* and *b*).

Tetrahedral, sub-triangular, 35–45 μ. Wall thin. Tetrad scar extending to the margin. Exospore reticulate; mesh 5–10 μ across, with deep alveoli and lamellae thin and projecting at the periphery up to 5 μ; around the apical crest ornamentation is absent, but towards the equatorial margin an incomplete reticulation of branching ridges is observable.

The spores of this species are mentioned by Spring (1849, p. 43).

L. diaphanum Sw. (fig. 49).

Tetrahedral, almost spherical, 30–35 μ. Wall thin. Tetrad scar extending to the margin. Exospore reticulate; mesh 5–10 μ, lamellae thin and projecting at the periphery from 5 to 7 μ; around the apical crest the ornamentation is absent, but towards the equatorial margin branched ridges are seen as in *L. contiguum* (fig. 50).

The spores of this species are mentioned and figured by Hooker and Greville (1831, tab. 227).

L. diffusum R. Br. (fig. 73).

Tetrahedral, almost spherical, 40–45 μ. Wall 4 μ in thickness. Tetrad scar extending to the margin. Exospore irregularly rugose; low ridges radiate from the apical crest, which is itself surrounded by a thickened border.

The spores of this species are mentioned by Spring (1849, p. 39).

L. Drummondii Spring (fig. 70).

Tetrahedral, sub-triangular, 50–55 μ. Wall 5 μ in thickness. Tetrad scar 2/3 radius. Exospore rugose, with irregular ridges uniting to form a mesh-like structure on the ab-apical side; the apical surface bears short, papillate ridges.

The spores of this species are mentioned by Spring (1849, p. 35).

L. fastigiatum R. Br. (figs. 72 *a* and *b*).

Tetrahedral, almost spherical, 35–40 μ. Wall thin. Tetrad scar 2/3 radius. Exospore irregularly reticulate; on the ab-apical side the ornamentation is a broken reticulum in which the lamellae have a tendency to enlarge at the ends and angles. Ornamentation is absent from the apical surface.

The spores of this species are mentioned by Spring (1849, p. 41).

L. inundatum L. (figs. 71 *a* and *b*).

Tetrahedral, sub-triangular, 45–50 μ. Wall thin. Tetrad scar 2/3 radius, situated in an unornamented furrow. Exospore reticulate; the reticulation is irregular and the lamellae wavy, particularly on the ab-apical side. On the apical surface the mesh structure is less obvious, decreasing around the furrow.

The spores of this species are described by Luerssen (1889) and figured by Pritzel (1901, fig. 371); they are described and figured by Wilson (1934, p. 18, Pl. 276) and by Erdtman (1943).

L. laterale R. Br. (figs. 56 *a* and *b*).

Tetrahedral, almost spherical, 50–65 μ. Wall thin. Tetrad scar 2/3 radius, conspicuous and bounded by a thickened ridge.

Exospore, on the ab-apical side, irregularly reticulate, mesh large, 10 μ or more, with thin lamellae and shallow lumina. The apical surface is covered with small, thin ridges alternating with elongate pits, giving a delicate veined appearance.

L. magellanicum Sw. (figs. 57 *a* and *b*).

Tetrahedral, sub-triangular, 45–50 μ. Wall thin. Tetrad scar extending to the margin. Exospore reticulate; on the ab-apical side the mesh is irregular, from 5 to 10 μ across and the lamellae 2 μ in thickness. Round the apical crest the reticulation is absent and the exospore is finely granular.

L. obscurum L. (figs. 69 *a* and *b*).

Tetrahedral, almost spherical, 30–35 μ. Wall thin. Tetrad scar 2/3 radius. Exospore reticulate on the ab-apical side; mesh 5–8 μ across and lamellae 1–2 μ in thickness; the apical surface is ornamented with a delicate, inconspicuous reticulum.

The spores of this species are described and figured by Wilson (1934, p. 19, Pl. 277).

L. paniculatum Desv. (figs. 62 *a* and *b*).

Tetrahedral, sub-triangular, 30–35 μ. Wall thin. Tetrad scar extending to the margin. Exospore reticulate; mesh 4–5 μ, lamellae thin and projecting 3 μ from the periphery; the apical surface is without ornamentation.

The spores of this species are mentioned by Spring (1842, p. 95).

L. phyllanthum Hook. & Arn. (fig. 66).

Tetrahedral, sub-triangular, 40–50 μ. Wall 3 μ in thickness. Tetrad scar extending to the margin. Exospore reticulate; mesh 5 μ, irregular with deep lumina and the lamellae uneven and wavy. The reticulation is less marked on the apical surface and absent around the crest.

The spores of this species are figured by Pritzel (1901, fig. 371); they are described and figured by Selling (1946, p. 15).

L. ramulosum Kirk (fig. 58).

Tetrahedral, almost spherical, 50 μ. Wall 5 μ in thickness. Tetrad scar 2/3 radius. Exospore reticulate on the ab-apical side; mesh 5–12 μ; the apical surface is finely channeled and pitted.

L. scariosum Forst. (fig. 52).

Tetrahedral, almost spherical, 30 μ. Wall thin. Tetrad scar extending to the margin. Exospore reticulate; mesh 5–10 μ, variable in diameter; lamellae thin and lumina shallow; ornamentation is absent from the apical surface.

L. Sprucei Baker (fig. 59).

Tetrahedral, almost spherical, 45–50 μ. Wall thin. Tetrad scar 2/3 radius, situated in an unornamented furrow. Exospore reticulate; on the ab-apical side a series of irregular anastomosing ridges form a coarse reticulum; on the apical surface a thin-walled delicate mesh structure is developed extending from the crest to the periphery.

L. spurium Willd. (fig. 68).

Tetrahedral, almost spherical, 35–40 μ. Wall thin. Tetrad scar extending to the margin. Exospore reticulate; on the ab-apical side the reticulum is irregular, frequently broken, with a mesh of from 5 to 7 μ; ornamentation is absent from the apical surface.

The spores of this species are mentioned by Spring (1849, p. 49).

L. vestitum Desv. (figs. 53 *a* and *b*).

Tetrahedral, almost spherical, 35–40 μ. Wall thin. Tetrad scar 2/3 radius. Exospore reticulate; on the ab-apical side the mesh measures 5–10 μ across and the thin lamellae project 5 μ at the periphery. On the apical surface the ornamentation is of short, irregularly shaped ridges.

L. volubile Forst. (fig. 54).

Tetrahedral, sub-triangular, 35–40 μ. Wall thin. Tetrad scar extending to the margin. Exospore irregularly reticulate on the ab-apical side; round the apical crest ornamentation is absent. A thin membranous frill, 5 μ deep, encircles the spore at the equator.

The spores of this species are mentioned by Hooker and Greville (1831, tab. 170), but their small figure shows no ornamentation.

L. Wightianum Wall. (fig. 51).

Tetrahedral, almost spherical, 40–45 μ. Wall thin. Tetrad scar extending to the margin. Exospore reticulate; mesh 5–10 μ, lamellae thin and projecting 5 μ from the periphery; ornamentation is absent from the apical furrow, but irregular ridges are developed towards the periphery as in *L. contiguum* (fig. 50).

Species of Lycopodium with Spinose Exospore.

L. densum La Billard. (figs. 75 *a* and *b*).

Tetrahedral, sub-triangular, 35–40 μ. Wall thin. Tetrad scar extending to the margin. Exospore on the ab-apical side covered with spinose processes, 3–5 μ long and spaced 5–7 μ apart. The apical surface is without ornamentation.

This is remarkable as the only species of Lycopodium which has been noted to have spinose ornamentation, giving an echinate appearance to the spores, a feature present in microspores of Selaginella.

The spores of this species are figured by Pritzel (1901, fig. 371).

GENUS II. PHYLLOGLOSSUM.

The single species of this genus *P. Drummondii* is found in Australia and New Zealand. It is a small plant, only a few centimetres high, with a short axis arising from an annually produced tuber. The axis terminates in a strobilus of the Urostachys type. Sporangia homosporous.

P. Drummondii Kunze (fig. 67).

Tetrahedral, sub-triangular, 35-40 μ. Wall thin. Tetrad scar extending to the margin. Exospore reticulate; mesh 5 μ, of irregular shape, lamellae 2 μ in thickness; round the apical crest ornamentation is absent.

The spores of this species are figured by Eames (1936, after Bertrand).

The resemblance of the two genera Lycopodium and Phylloglossum, especially in the structural features of the strobilus, probably indicates a close relationship. Phylloglossum is regarded by Eames (1936) as a "reduced Lycopod", which has become adapted structurally to the "tuberous perennial" habit. "It is not a simple and extremely primitive plant but one whose apparent simplicity is the result of specialisation."

It is of interest to note that the spores of Phylloglossum resemble closely those of *Lycopodium phyllanthum* (fig. 66), and by reason of the similarity, the species has been included in the key to Group IV of the *Lycopodiaceae.*

SPORE STRUCTURE IN LYCOPODIACEAE.

From the foregoing account of spore morphology in the *Lycopodiaceae* it becomes of interest to consider to what extent spore characters may contribute to any scheme of classification, and how far the spore types may be correlated with the habit and phytogeography of the species. The most recent systematic arrangement of Walton and Alston (1938), which recognises six sub-genera, will be examined from this point of view.

Sub-genus I, UROSTACHYS, which includes the largest number of species (71), is divided into three sections. In Section 1, *Selago*, the species are of the erect, terrestrial type, while Sections 2 and 3, *Subselago* and *Phlegmaria*, contain the epiphytic, pendent species. All species of the sub-genus UROSTACHYS are characterised by the possession of a pitted exospore. The pits are various in size and shape, and the exospore may be finely pitted or exhibit coarse irregular pits. In the majority of species the pits are small and round, averaging 2–3 μ in diameter, some closely set together and others widely spaced. But no particular type of pitting is characteristic of any one of the three sections of the sub-genus, and it cannot be claimed that the exospore ornamentation bears any relationship either to epiphytism or edaphic conditions. Nor is there any correlation with geographical distribution, since in the sub-genus UROSTACHYS, tropical, temperate and arctic species are included.

In the six species of the *Selago* section, however, *L. ceylanicum* (fig. 5), *L. fontinaloides* (fig. 2), *L. lucidulum* (fig. 6), *L. miniatum* (fig. 4), *L. Selago* (fig. 1) and *L. serratum* (fig. 3), the spores have a characteristic shape, exhibiting straight or slightly concave sides and truncate angles. This shape has been noted in no other sub-genus of the family, and the six species referred to above comprise the group of *L. Selago* of the present author.

The remaining five sub-genera of Walton and Alston include species which are all terrestrial, with prostrate stems, and the species have a wide geographical distribution. Pritzel (1901) united these five sub-genera in his sub-genus RHAPALOSTACHYS, and, as he recognised, all species included have spores with reticulate ornamentation of the exospore, with one exception, *L. densum* (fig. 75), in which the spore wall is spinose. The reticulation varies from a small regular mesh with thin lamellae to a large mesh with lamellae of varying thickness. The regular network may be replaced by a pseudo-reticulum of irregular, sinuous ridges as in *L. carolinianum* (fig. 74) and *L. diffusum* (fig. 73).

In Sub-genus II, CLAVATOSTACHYS, the mesh of the reticulum averages from 5 to 10 μ. The spores are characterised by having an apical surface which is either smooth or finely pitted, or with short, irregular ridges which may extend inwards for a short distance from the margin or unite to form an irregular network around the apical crest.

Sub-genus III, COMPLANATOSTACHYS, comprises six species in which the spore morphology lacks uniformity. Four species, *L. complanatum* (fig. 63), *L. scariosum* (fig. 52), *L. volubile* (fig. 54) and *L. Wightianum* (fig. 51), are typically reticulate on the ab-apical hemisphere, and with sculpturing poorly developed or absent on the apical side. *L. carolinianum* (fig. 74), with irregular sinuous ridges uniting in a network, has a characteristic appearance reminiscent of *L. inundatum* (fig. 71), with which Wilson (1934) suggests the species might justifiably be grouped. *L. casuarinoides* (fig. 12) is exceptional in having a finely pitted exospore.

Sub-genus IV, CERNUOSTACHYS, includes three species all with differing forms of sculpturing, and one is the exceptional spinose spore type of *L. densum* (fig. 75). The other two species, *L. cernuum* (fig. 65) and *L. obscurum* (fig. 69), have spores which are reticulate on the ab-apical face, and on the apical surface *L. cernuum* is papillose while *L. obscurum* has a delicate mesh.

Sub-genus V, INUNDATOSTACHYS, includes the three species *L. inundatum* (fig. 71), *L. adpressum* (fig. 64) and *L. Drummondii* (fig. 70). All three possess a tetrad scar which lies in a furrow surrounded by a clear unornamented area. The ab-apical surface is irregularly reticulate, and on the apical side this network is replaced by uneven papillae or ridges.

Sub-genus VI, LATERALOSTACHYS, contains the two species *L. diffusum* (fig. 73) and *L. laterale* (fig. 56), which are quite dissimilar, the former rugose and ridged, and the latter exhibiting a wide-meshed network on the ab-apical side, while on the apical it is finely channeled.

It is apparent, therefore, that in Lycopodium the spore morphology adds supporting evidence to the taxonomy of the genus only in a general way. Nevertheless, it should be admitted that Pritzel's division into two sub-genera, based on spore characters, is more easily maintained than the division into six sub-genera, since the spores fall definitely into two major well-defined groups, the pitted and the reticulate. Such characteristic ornamentation easily distinguishes the spores of Lycopodium and Phylloglossum from those of other members of the LYCOPODIINAE, and it has been employed as the basis of division into the groups which have been suggested in the foregoing pages.

There is no apparent connection between spore sculpturing on the one hand and ecological conditions on the other; nor is there any obvious biological signification either in the pitted or reticulate pattern of the exospore.

SELAGINELLACEAE.

General Characters and Classification.

The family *Selaginellaceae* comprises a single genus with over 600 species. While they exhibit a considerable variety of growth form, in most species the shoot system is usually creeping and dorsiventral with small leaves arranged in four ranks. The leaves and sporophylls are ligulate, and the sporangia, usually borne in distinct strobili, are of two types, the plants being heterosporous.

The genus has a world-wide distribution, but most of the species grow in damp forests of tropical regions and are essentially hygrophilous. Some xerophilous species, however, are able to withstand desiccation for months; the stems curl up when dry and expand when moistened.

One of the earliest classifications of the genus was that of Spring (1849), who distinguished two main groups which he designated:

Section I. *Homoeophylla*, species with leaves all alike.
Section II. *Heterophylla*, species with leaves dimorphous.

The later section, which contains the larger number of species [illegible] subdivided according to the nature of the strobilus and the morphological character of the stems and leaves.

Spring was followed by Baker (1887), who advanced a [illegible] detailed and elaborate arrangement in "Handbook of the Fern-Allies" and recognised four sub-genera as follows:

Sub-genus I. *Selaginella* proper, with ordinary leaves all alike. This is virtually the same as Spring's Section *Homoeophylla*.
Sub-genus II. *Stachygynandrum*, with dimorphous leaves and uniform sporophylls. This sub-genus contains the largest number of species (259), and Baker divides it into six series. The species within the series are classified, first, according to habit, and secondly, according to the arrangement of the stems, leaves and rhizophores.
Sub-genus III. *Homostachys*, with dimorphous leaves and sporophylls.
Sub-genus IV. *Heterostachys*, with dimorphous leaves and sporophylls; spikes resupinate.

The arrangement adopted by Hieronymous (1901) resembled more closely that of Spring, having the same two sub-genera, *Homoeophylla* and *Heterophylla*, the latter being subdivided on the basis of a complicated system depending mainly on the anatomy of the stems and leaves. The account given by Hieronymous covers some 440 species, but only slight reference is made to spore morphology and only a few species are figured.

The most recent classification is that of Walton and Alston (1938), whose treatment of the genus bears a close resemblance to that of Baker, maintaining the four sub-genera of that author, and retaining the six series within the sub-genus *Stachygynandrum.* The names of the series are altered in some instances, and there is also some modification in the serial grouping of the species, but the main variant from Baker's arrangement is in placing together all species with articulate stems in the series *Articulatae.*

The salient features of the classification put forward by Walton and Alston are as follows:—

Sub-genus I. EUSELAGINELLA. Leaves and sporophylls uniform.
  1. Group of *S. selaginoides.* Sporophylls spirally arranged.
  2. Group of *S. pygmaea.* Strobili tetragonous.
  3. Group of *S. uliginosa.* Strobili tetragonous. Leaves decussate.
  . Group of *S. rupestris.* Strobili tetragonous. Leaves linear, spirally arranged.

Sub-genus II. STACHYGYNANDRUM. Leaves dimorphous, sporophylls uniform.
  Series 1. *Decumbentes.* Prostrate species with main stems rooting throughout.
  Series 2. *Ascendentes.* Suberect species, often with a single banded stele.
  Series 3. *Sarmentosae.* Suberect, scandent or rarely prostrate, polystelic species.
  Series 4. *Caulescentes.* Erect species. The simple erect part of the stem is usually homophyllous and the branched part heterophyllous.
  Series 5. *Circinatae.* Xerophilous species.
  Series 6. *Articulatae.* Tropical American species with articulate stems.

Sub-genus III. HOMOSTACHYS. Leaves dimorphous. Species with creeping stems and loose strobili.

Sub-genus IV. HETEROSTACHYS. Heterophyllous species with strongly dimorphous sporophylls.

In a genus with such a vast number of species as Selaginella it is obviously difficult, if not impossible, to devise a wholly satisfactory classification. This has been clearly indicated by Weatherby (1944) in his discussion of the group of *Selaginella Oregana,* where he says:

"In any division of Selaginella based on habit, parallel leaf- and spore-variations will be found in different groups. But in any division based on leaf- or spore-characters, parallel variation in habit and other features will be found to quite as great an extent. And as a primary basis for systematic arrangement, habit has very real and practical virtues—so much so that, within the two great homoeophyllous and heterophyllous sub-genera, it has been used by all taxonomists up to the present time." In the same connection Weatherby draws attention to the usefulness of the characters of both megaspores and microspores in defining a species, but he adds a note of caution, since the appearance of the sculpturing varies with age, although the pattern is constant within the species in mature forms.

No detailed treatment of the megaspores has been attempted here, as they are not used extensively in spore analysis of coals, and the primary object of the present study is to elucidate the features of importance in spore morphology which have a bearing on fossil spore classification. It is worthy of note, however, that the megaspores vary in size from $1\frac{1}{2}$ to 5 mm. in diameter, and their sculpturing is of several types—tuberculate, spinose or reticulate. There is no noticeable relationship between the ornamentation of the megaspore and that of the microspore of the same species; for example, a microspore may be furnished with an equatorial flange, whereas the megaspore in the same plant may have a coarsely tuberculate exospore.

The following account deals with the microspores only, and a short description is given of as many species as it has been possible to obtain the sporangial material, about 350 in all. As in the genus Lycopodium the species are arranged in groups based on spore characters; the several types of spore sculpturing are illustrated, and under the specific descriptions references are made to the appropriate figures. Where mention of the spores has been made by earlier writers the reference is given; the number after references to Hieronymous (1901) is that which he has given to the particular species under review.

Genus I. SELAGINELLA.

Key to Groups in Selaginella.

A. Spores bearing a membranous wing, flange or annular ring in the equatorial region.
  B. Membrane encircling the spore body and having an equatorial expansion . I. Group Sibirica

BB. Membrane not encircling the spore body.	
C. Spores with an annular ring . .	IV. Group Scandens
CC. Spores with membranous equatorial flange.	
D. Flange notched, 5–10 μ wide . .	II. Group Sanguinolenta
DD. Flange undulate or fimbriate; membrane strutted . . .	III. Group Megastachys
AA. Spores without equatorial wing or flange.	
B. Spore margin entire.	
C. Exospore smooth, without ornamentation	V. Group Firmula
CC. Exospore granular	VI. Group Helvetica
BB. Spore margin uneven.	
C. Spore margin crenulate . . .	VII. Group Cathedrifolia
CC. ,, margin sinuate, toothed or with apparent processes.	
D. Ornamentation of blunt processes.	
E. Processes low, rounded and broader than long.	
F. Processes 2–5 μ broad at base.	
G. Processes small, closely set, 1–3 μ apart . . .	IX. Group Leptophylla
GG. Processes set 2–5 μ apart .	VIII. Group Radicata
FF. Processes 3–8 μ broad at base.	
G. Processes irregularly spaced, 2–5 μ apart . . .	X. Group Vaginata
GG. Processes flat, close set, separated by channels .	XI. Group Repanda
EE. Processes thin, rod-like, longer than broad.	
F. Rod-like processes, 2–5 μ long.	
G. Processes densely packed .	XII. Group Stolonifera
GG. ,, sparsely packed .	XIII. Group Biformis
FF. Rod-like processes 5–10 μ long	XIV. Group Latifrons
DD. Ornamentation of pointed processes.	
E. Processes thin, acicular, 3–8 μ long, set 5–10 μ apart . .	XVIII. Group Magnifica
EE. Processes with base 2 μ or more broad.	
F. Stout conical processes, base 5 μ or more broad.	
G. Long curved spines . .	XX. Group Kraussiana
GG. Straight spines 5–10 μ long .	XIX. Group Selaginoides
FF. Spinose processes with base 2 μ.	
G. Spines widely spaced, 5–8 μ apart	XV. Group Sub-arborescens
GG. Spines densely packed 2–5 μ apart.	
H. Spines short, 1–3 μ long .	XVI. Group Anceps
HH. ,, long, 4–7 μ . .	XVII. Group Uncinata

GROUP I. GROUP OF S. SIBIRICA.

Spores having a central spore body surrounded and enclosed by a thin transparent membrane. The surface of the membrane may be smooth, granular, pitted or setose; it is frequently wrinkled and folded. In optical section the membrane appears as an equatorial wing varying in width from 3 to 15 μ, averaging between 5 and 10 μ.

The species of Selaginella in which the spores conform to the "Rupestris Type" have been recorded only from the sub-genus *Euselaginella* (as defined by Walton and Alston, 1938), excepting their Group I of *S. selaginoides*. This is equivalent to the sub-genus *Homoeophyllum*, Section II, *Tetrastachys*, of Hieronymous (1901). These authorities recognise three distinct groups in this section of the sub-genus:

1. Group of *S. pygmaea* (syn. *S. pumila*) with 2 species.
2. Group of *S. uliginosa* with 2 species.
3. Group of *S. rupestris* with over 40 species.

The spores of these three groups have been found by the present author to be morphologically similar and are therefore classed together in one and the same group, *S. sibirica*. Among some species the microspores are closely similar and distinguishing characters difficult to define.

Key to the Species.

A. Spores in which the membrane is inconspicuous or narrow, not exceeding 7 μ in width.	
B. Surface of the membrane without ornamentation.	
C. Total spore diameter 35–45 μ	*S. Schmidtii* *S. uliginosa*, fig. 76
CC. ,, ,, ,, 40–55 μ	*S. rupestris* *S. sibirica*, fig. 77 *S. Standleyi*
BB. Surface of membrane with ornamentation.	
C. Surface of membrane granular.	
D. Surface finely granular. Average size 40–50 μ	*S. acanthonota* *S. arenicola*, fig. 78 *S. densa* *S. mutica* *S. Riddellii* *S. Underwoodii* *S. Watsoni*
DD. Surface coarsely granular. Membrane wrinkled and folded. Average size 45–55 μ	*S. Bigelowii* *S. leucobryoides* *S. Parishii* *S. scopulorum* *S. Sheldoni* *S. strutholoides*, fig. 79
CC. Surface setose	*S. pygmaea*, fig. 80
AA. Spores in which the membrane projects 7–10 μ or more from the spore surface.	
B. Surface coarsely granular. Average size 50–60 μ .	*S. Dregei* *S. echinata* *S. Hanseni* *S. peruviana* *S. rupicola* *S. Sartorii* *S. Wallacei*, fig. 81 *S. Wrightii*
B. Surface pitted	*S. Preissiana*, fig. 82

S. acanthonota Underw.

Sub-triangular to round, total diameter 40–50 μ, a few specimens larger. Tri-radiate mark extending to the margin. Central spore body, 30–35 μ, surrounded by a thin, granular membrane, projecting from the spore surface 5–7 μ.

The spores of this species are referred to by Clausen (1946).

S. arenicola Underw. (fig. 78).

Sub-triangular, total diameter 35–45 μ. Tri-radiate mark extending to the margin. Central spore body, 25–30 μ, surrounded by a thin, granular membrane, projecting 5–7 μ from the spore surface and with a narrow (2 μ) clear translucent border.

The spores of this species are mentioned by Hieronymous (1901, 11) and by Clausen (1946).

S. Bigelowii Underw.

Sub-triangular to spherical, total diameter 50–60 μ. Tri-radiate mark extending to the margin. Central spore body, 30–35 μ, surrounded by a thin, finely granular membrane, projecting from the spore surface 7–10 μ.

The spores of this species are mentioned by Hieronymous (1901, 9).

S. densa Rydb.

Spherical, total diameter 45–60 μ. Tri-radiate mark extending to the margin. Central spore body, 30–40 μ, surrounded by a thin, finely granular membrane, projecting from the spore surface 7–10 μ.

S. Dregei (Presl.) Hieron.

Almost spherical, total diameter 65–75 μ. Tri-radiate mark extending to the margin. Central spore body, 45–55 μ, surrounded by a thin, coarsely granular, much folded membrane projecting 10–15 μ from the spore surface, and with a translucent border (2 μ).

S. echinata Baker

Sub-triangular to spherical, total diameter 50–65 μ. Tri-radiate mark extending to the margin. Central spore body, 35–45 μ, surrounded by a thin, granular, much folded membrane projecting from the spore surface 7–10 μ.

S. Hanseni Hieron.

Sub-triangular to spherical, total diameter 50–60 μ. Tri-radiate mark extending to the margin. Central spore body, 30–40 μ, surrounded by a thin, coarsely granular membrane projecting from the spore surface 7–10 μ.

The spores of this species are mentioned by Hieronymous (1901, 40).

S. leucobryoides Maxon.

Sub-triangular to round, total diameter 40–50 μ. Tri-radiate mark extending to the margin. Central spore body, 30–40 μ, surrounded by a thin, finely granular, much folded membrane projecting from the spore surface 5 μ.

S. mutica Eaton

Sub-triangular, total diameter 40–50 μ. Tri-radiate mark extending to the margin. Central spore body, 35–45 μ, surrounded by a thin, finely granular, much folded membrane projecting 5–7 μ from the spore surface.

The spores of this species are mentioned by Hieronymous (1901, 12) and Weatherby (1944).

S. Parishii Underw.

Sub-triangular, total diameter 45–60 μ. Tri-radiate mark 1/3 radius. Central spore body, 35–45 μ, surrounded by a thin, coarsely granular, wrinkled membrane projecting 5–7 μ from the spore surface.

S. peruviana (Milde) Hieron.

Sub-triangular to spherical, total diameter 55–65 μ. Tri-radiate mark extending to the margin. Central spore body 35–45 μ, surrounded by a thin, coarsely granular, much folded membrane projecting 10 μ from the spore surface.

The spores of this species are mentioned by Hieronymous (1901, 34).

S. Preissiana Spring (fig. 82).

Sub-triangular to spherical, total diameter 40–50 μ. Tri-radiate mark extends almost to the margin. Central spore body, 25–30 μ, surrounded by a thin, finely pitted membrane projecting from the spore surface 7–10 μ.

The spores of this species are mentioned by Spring (1849, p. 61) and Hieronymous (1901, 5).

S. pygmaea Kaulf. (*S. pumila* Spring) (fig. 80).

Spherical, total diameter 50–60 μ. Tri-radiate mark extending to the margin. Central spore body, 35–45 μ, surrounded by a thin membrane ornamented with stiff bristles about 3 μ long and set

2–3 μ apart; the membrane projects 5–7 μ from the spore surface. There is a tendency for the spores to remain united in tetrads.

The spores of this species are mentioned by Kaulfuss (1824, p. 9), Spring (1849, p. 60) and Hieronymous (1901, 3).

S. Riddellii van Eseltine

Sub-triangular, total diameter 40–50 μ. Tri-radiate mark extends to the margin. Central spore body, 35–45 μ, surrounded by a thin, finely granular, much folded membrane projecting 3–5 μ from the spore surface.

The spores of this species are referred to by Clausen (1946).

S. rupestris Spring

Spherical, total diameter 45–55 μ. Tri-radiate mark extends almost to the margin. Central spore body, 30–40 μ, surrounded by a thin, nearly smooth, wrinkled membrane projecting 5–7 μ from the surface of the spore body.

The spores of this species are referred to by Milde (1859, who defines 10 varieties), Hieronymous (1901, 19), Lyon (1901), Reeve (1935, Pl. 380), Knox (1938, fig. 24) and Clausen (1946). Reeve notes the occurrence of "dumb-bell" spores which he figures; these have not been seen by the present author.

S. rupicola Underw.

Sub-triangular, total diameter 45–60 μ. Tri-radiate mark extending to the margin. Central spore body, 30–40 μ, surrounded by a thin, granular membrane projecting 7–10 μ from the spore surface, and with a narrow (2 μ) translucent rim.

The spores of this species are mentioned by Hieronymous (1901, 8).

S. Sartorii Hieron.

Sub-triangular, total diameter 50–65 μ. Tri-radiate mark extends to the margin. Central spore body, 30–45 μ, surrounded by a thin, coarsely granular, much folded membrane projecting 10 μ from the spore surface, with a clear narrow (2 μ) border and an undulating margin due to the irregular folding of the membrane.

The spores of this species are mentioned by Hieronymous (1901, 38).

S. Schmidtii Hieron.

Sub-triangular to spherical, total diameter 35–50 μ. Tri-radiate mark extends to the margin. Central spore body, 30–40 μ, surrounded by a thin, smooth, wrinkled membrane projecting from the spore surface 3–5 μ.

The spores of this species are mentioned by Hieronymous (1900, p. 292; 1901, 16).

S. scopulorum Maxon

Almost spherical, total diameter 40–50 μ. Tri-radiate mark extending to the margin. Central spore body, 30–40 μ, surrounded by a thin, finely granular membrane projecting from the spore surface 5 μ.

S. Sheldoni Maxon

Sub-triangular to spherical, total diameter 45–55 μ. Tri-radiate mark 1/3 to 2/3 radius. Central spore body, 30–40 μ, surrounded by a thin, granular, much folded membrane projecting 5–7 μ from the spore surface.

S. sibirica (Milde) Hieron. (fig. 77).

Sub-triangular, total diameter 45–55 μ. Tri-radiate mark 2/3 radius. Central spore body, 35–40 μ, surrounded by a thin, smooth, much folded membrane projecting 5–7 μ from the spore surface.

The spores of this species are mentioned by Hieronymous (1901, 22).

S. Standleyi Maxon

Sub-triangular to spherical, total diameter 40–50 μ. Tri-radiate mark extending to the margin. Central spore body, 35–40 μ, surrounded by a thin, almost smooth, much folded membrane projecting 3–5 μ from the spore surface.

S. strutholoides (Presl.) Underw. (fig. 79).

Sub-triangular, total diameter 50–65 μ. Tri-radiate mark extending to the margin. Central spore body, 40–50 μ, surrounded by a thin, finely granular, much folded membrane projecting 5 μ from the spore surface.

The spores of this species are referred to by Weatherby (1944).

S. uliginosa Spring (fig. 76).

Spherical, total diameter 35–50 μ. Tri-radiate mark extending to the margin. Central spore body, 30–40 μ, surrounded by a thin, smooth, much folded membrane projecting 3–5 μ from the spore surface.

The spores of this species are mentioned by Hieronymous (1901, 6).

S. Underwoodii Hieron.

Sub-triangular to spherical, total diameter 40–55 μ. Tri-radiate mark extending to the margin. Central spore body, 35–40 μ, surrounded by a thin, finely granular, much folded membrane projecting 5–7 μ from the spore surface.

The spores are mentioned by Hieronymous (1901, 37) and Weatherby (1944).

S. Wallacei Hieron. (fig. 81).

Sub-triangular to spherical, total diameter 55–70 μ. Tri-radiate mark extending almost to the margin. Central spore body, 45–50 μ, surrounded by a thin, coarsely granular membrane projecting 7-10 μ from the spore surface.

The spores of this species are mentioned by Hieronymous (1901, 23).

S. Watsoni Underw.

Sub-triangular to spherical, total diameter 40–50 μ. Tri-radiate mark 2/3 radius. Central spore body, 30–40 μ, surrounded by a thin, granular, folded membrane projecting 5–7 μ from the spore surface.

The spores of this species are mentioned by Hieronymous (1901, 14, fig. 402, J).

S. Wrightii Hieron.

Sub-triangular to spherical, total diameter 45–65 μ. Tri-radiate mark 2/3 radius. Central spore body, 35–45 μ, surrounded by a thin, granular, much folded membrane projecting from the spore surface 10 μ. The margin of the membrane is sinuous, due to folds.

The spores of this species are mentioned by Hieronymous (1901, 24).

Group II. GROUP OF S. SANGUINOLENTA

The spores of this group are characterised by the presence of an equatorial flange which may be almost entire, irregularly notched or serrate, projecting 5–10 μ from the surface of the spore body. The ab-apical hemisphere is covered by a thin wrinkled membrane or ornamented with irregular angular elevations. The apical surface may be smooth, granular or scabrid. The size of the spore body varies from 25 to 50 μ in diameter.

Key to the Species.

A. Ab-apical hemisphere with an irregular folded membrane.
  B. Total diameter of spore 25–45 μ.
    C. Total diameter 25–35 μ . . . . *S. laevigata*, fig. 83
      S. Lyallii
      S. valdepilosa, fig. 84
    CC. ,, ,, 35–45 μ . . . . *S. saccharata*, fig. 85

BB. Total diameter of spore 45–60 μ.	
C. Total diameter 45–50 μ	*S. Aitchisonii*
CC. ,, ,, 50–60 μ	*S. sanguinolenta* fig. 86
AA. Ab-apical hemisphere with irregular angular elevations.	
B. Total diameter 35–45 μ; elevations warty . .	*S. borealis*, fig. 87 *S. Jacquemontii*
BB. ,, ,, 30–35 μ.	
C. Elevations serrate	*S. pedata*, fig. 88
CC. ,, blunt, tuberculate	*S. stenophylla*, fig. 89

S. Aitchisonii Hieron.

Sub-triangular, spore body 35–45 μ, total diameter 45–55 μ. Tri-radiate mark extending to the margin. The apical crest is conspicuous and the apical surface is finely granular. The ab-apical hemisphere is covered by a thin wrinkled membrane which forms a notched flange round the equator, 5–7 μ in depth.

Alston (1945 *a*) indicates that this species is a variety of *S. sanguinolenta* (fig. 86); the spores of both are closely similar. The spores are described by Hieronymous (1901, 44, and 1902, p. 171).

S. borealis (Kaulf.) Spring (fig. 87).

Tetrahedral, sub-triangular, spore body 30–40 μ, total diameter 35–45 μ. Tri-radiate mark extending to the margin. The exospore on the ab-apical surface is ornamented with irregular, warty processes; on the apical side the spore is almost smooth. In the equatorial plane a flange with notched rim is developed.

The spores are mentioned by Kaulfuss (1824, p. 18) and Hieronymous (1901, 45).

S. Jacquemontii Spring

Tetrahedral, sub-triangular to spherical, spore body 30–45 μ, total diameter 40–55 μ. Tri-radiate mark extending to the margin. Ab-apical hemisphere surrounded by a thin membrane with uneven warty ridges. The membrane projects beyond the spore body and is seen as an equatorial flange with an irregular edge. The spores of this species are very similar to those of *S. borealis* (fig. 87); Baker (1887) considers this a synonym and close ally to *S. sanguinolenta*, whereas Alston (1945 *a*) maintains it is a form of *S. sanguinolenta* (fig. 86).

The spores of this species are described by Spring (1849, p. 194) and Hieronymous (1901, 45).

S. laevigata Baker (figs. 83 *a* and *b*).

Sub-triangular, spore body 25–30 μ in diameter. Tri-radiate mark extends almost to the margin; apical crest conspicuous and with a narrow flange; apical surface granular. The ab-apical hemisphere is covered with a thin, finely wrinkled membrane which appears at the equator as a transparent wing 5 μ in width.

The spores of this species are mentioned by Hieronymous (1901, 372).

S. Lyallii (Hk. & Gr.) Spring

Sub-triangular, spore body 30–35 μ in diameter. Tri-radiate mark extends to the margin; apical surface granular. The ab-apical hemisphere is covered by a thin, finely wrinkled membrane, which projects beyond the spore margin 5 μ and appears as an equatorial wing. The spores of this species resemble those of *S. laevigata* (fig. 83) in all essentials. They are described and figured by Hieronymous (1901, 394, fig. 408).

S. pedata Klotzsch (figs. 88 *a* and *b*).

Sub-triangular, spore body 25–35 μ in diameter. Tri-radiate mark extends to the margin; apical surface and crest scabrid. The ab-apical hemisphere bears irregularly serrate, rigid emergences. The equatorial ring is similarly unevenly serrate.

The spores of this species are described by Hieronymous (1901, 408).

S. saccharata A. Br. (fig. 85).

Tetrahedral, sub-triangular, spore body 30–40 μ, total diameter 35–45 μ. Tri-radiate mark 2/3 radius. On the apical side the exospore is ornamented with large coarse, irregular, tuberculate processes; the ab-apical surface is covered by a folded membrane which appears at the equator as a transparent notched wing-like extension from the spore wall.

The spores are described by Hooker and Greville (1831, II, tab. 177) under the synonym, *L. ovalifolium*, and also by Hieronymous (1901, 181, and 1902).

S. sanguinolenta (L.) Spring (fig. 86).

Sub-triangular to almost spherical, spore body 40–50 μ, total diameter 50–60 μ. Tri-radiate furrow frequently open and extending to the margin. The apical crest is conspicuous and the apical surface is smooth to finely granular. The ab-apical hemisphere is covered by a thin, wrinkled membrane which is seen at the equator as an uneven notched flange projecting 5 to 10 μ from the spore margin.

The spores are mentioned by Spring (1849, p. 57) and Hieronymous (1901, 43).

S. stenophylla A. Br. (figs. 89 *a* and *b*).

Sub-triangular, spore body 25 μ in diameter. Tri-radiate mark extends to the margin; apical surface smooth. The ab-apical hemisphere is ornamented with low, irregular, blunt elevations, 2–3 μ across and 3–4 μ apart. An uneven notched equatorial ring, 3–4 μ in width, is a conspicuous feature of the spores.

The spores of this species are described by Hieronymous (1901, 184).

S. valdepilosa Baker (figs. 84 *a* and *b*).

Sub-triangular, spore body 20–25 μ, total diameter of 25–30 μ. Tri-radiate mark 2/3 radius. The ab-apical hemisphere is covered by a thin membrane thrown into irregular folds which form a notched flange round the equator. The apical surface is granular.

Group III. GROUP OF S. MEGASTACHYS.

Spores with a spore body 25–40 μ in diameter. The ab-apical hemisphere is covered by a thin, transparent membrane, thrown into folds which frequently assume an areolate arrangement, supported by stout strengthening struts. In optical section this membrane projects beyond the spore surface from 5 to 12 μ, and has often a fimbriate margin. The conspicuous apical crest has either a serratulate margin or bears a membranous flange. The apical surface may be granular, or furnished with small, rigid, more or less triangular emergences.

The spores of this group are very similar, and extremely difficult to distinguish from one another, the nature of the apical crest being the only definite feature by which a few species can be segregated.

Key to the Species.

A. Species in which the apical crest bears a membranous flange.	
B. Spore body 25–30 μ in diameter . . .	*S. Mayeri*, fig. 90 *S. quatemalensis*
BB. ,, ,, 35–40 μ in diameter . . .	*S. tylophora*, fig. 91
AA. Species in which the apical crest is serratulate.	
B. Spore body 25–30 μ in diameter . . .	*S. Helferi* *S. integerrima*, fig. 92
BB. ,, ,, 30–40 μ in diameter . .	*S. asperula*, fig. 93 *S. flaccida*, fig. 94 *S. Lobbii* *S. megastachya*, fig. 96 *S. Ostenfeldii* *S. pseudo-prolifera* *S. Schlechteri* *S. semicordata*, fig. 97 *S. Usterii* *S. Willdenovii*, fig. 95

S. asperula vA. vR. (fig. 93).

Sub-triangular, tetrahedral, spore body 30–35 μ in diameter. Tri-radiate mark extends almost to the margin; apical crest and apical surface scabriolate. The ab-apical surface is covered by a thin, transparent membrane thrown into folds, supported by strengthening struts.

The spores of this species are mentioned by Spring (1849, p. 225) and Hieronymous (1901, 411).

S. flaccida Spring (fig. 94).

Sub-triangular, tetrahedral, spore body 30-35 μ in diameter. Tri-radiate mark extends to the margin; apical crest and apical surface are scabrid as in *S. asperula* (fig. 93). The ab-apical hemisphere is covered by a thin, transparent membrane, folded and strengthened by struts; the membrane projects beyond the spore body as a wing at the equator about 10 μ, and has a fimbriate border.

The spores of this species are mentioned by Hieronymous (1901, 348).

S. Helferi Warb.

Sub-triangular, tetrahedral, spore body 25–30 μ in diameter. Tri-radiate mark extends to the margin; the apical crest and the apical surface are both furnished with small, irregular, rigid, triangular emergences. On the ab-apical hemisphere the exospore bears stick-like processes 7–10 μ long, which act as struts for a thin, much folded membrane which covers the surface.

The spores of this species are described by Hieronymous (1901, 373).

S. integerrima Spring (figs. 92 *a* and *b*).

Sub-triangular, tetrahedral, spore body 25–30 μ in diameter. Tri-radiate mark extends to the margin; apical crest and apical surface scabrid. The ab-apical hemisphere is covered by a thin membrane thrown into folds and with a few supporting struts; the membrane projects about 10–15 μ from the surface of the spore.

The spores of this species are mentioned by Spring (1849, p. 79).

S. Lobbii Moore

Sub-triangular, tetrahedral, spore body 35–40 μ in diameter. Tri-radiate mark extends to the margin; the apical surface is scabriolate. The ab-apical hemisphere is covered by a thin membrane thrown into folds which assume an areolate form and bear strengthening struts. The spores of this species resemble closely those of *S. semicordata* (fig. 97); they are described by Hieronymous (1901, 369).

S. Mayeri Hieron. (figs. 90 *a* and *b*).

Sub-triangular, tetrahedral, spore body 25–30 μ in diameter. Tri-radiate mark extends to the margin; the apical crest has a conspicuous wing-like flange. The ab-apical hemisphere is covered by a thin membrane thrown into folds, occasionally strengthened by supporting struts, arranged in a pseudo-reticulate manner.

The spores of this species are described by Hieronymous (1901, 343).

S. megastachya Baker (figs. 96 *a* and *b*).

Sub-triangular, tetrahedral, spore body 30–40 μ in diameter. Tri-radiate mark extends to the margin; the apical crest and apical surface are scabrid. The ab-apical hemisphere is covered by a thin membrane, supported by hook-like structures; at the equator the membrane projects beyond the spore as an irregularly dissected wing up to 12 μ and has a fimbriate border.

The spores of this species are described by Hieronymous (1901, 361) and figured by Knox (1938, fig. 25).

S. Ostenfeldii Hieron.

Sub-triangular to spherical, spore body 30–40 μ in diameter. Tri-radiate mark extending to the margin; apical crest and apical surface scabrid. The ab-apical hemisphere is covered by a thin membrane, irregularly folded and supported by strengthening struts; it projects from the spore surface 10 μ, and has a fimbriate border.

S. pseudo-prolifera Hdl.-Mzt.

Sub-triangular to spherical, spore body 30–35 μ in diameter. Tri-radiate mark extending to the margin; apical crest and apical surface scabrid. The ab-apical hemisphere is covered by a thin membrane thrown into irregular folds, supported by struts and projecting 10 μ from the spore surface.

S. quatemalensis Baker

Sub-triangular to spherical, spore body, 25–30 μ in diameter. Tri-radiate mark extending to the margin; apical crest conspicuous and bearing a flange. The ab-apical hemisphere is covered by a thin membrane irregularly folded, assuming an areolate pattern and supported by struts; the membrane projects 5–10 μ beyond the spore margin.

The spores of this species are mentioned by Hieronymous (1901, 186).

S. Schlechteri Hieron.

Sub-triangular to spherical, spore body 35–40 μ in diameter. Tri-radiate mark extending to the margin; apical crest and apical surface scabrid. The ab-apical hemisphere is covered by a thin, folded membrane supported by struts and projecting 10–12 μ from the spore margin.

S. semicordata Spring (figs. 97 *a* and *b*).

Sub-triangular, tetrahedral, spore body 30–40 μ in diameter. Tri-radiate mark extending to the margin; apical crest and apical surface scabrid. The ab-apical hemisphere is covered by a thin, much folded membrane supported by hook-like struts. The edge of the membrane is fimbriate and projects beyond the spore margin from 10 to 15 μ.

The spores of this species are mentioned by Hieronymous (1901, 345).

S. tylophora vA. vR. (figs. 91 *a* and *b*).

Sub-triangular to spherical, spore body 35–40 μ in diameter. Tri-radiate mark extends to the margin; the apical crest bears a flange, and the apical surface is ornamented by minute, scattered spines. The ab-apical hemisphere is covered by a thin membrane thrown into folds arranged in an areolate manner and supported by struts; the membrane has a fimbriate edge and projects 10 μ beyond the spore margin.

S. Usterii Hieron.

Sub-triangular, spore body 30–35 μ in diameter. Tri-radiate mark extends to the margin; the apical crest and apical surface are scabrid. The ab-apical hemisphere is covered by a thin membrane supported by struts of varying length; the membrane projects beyond the spore margin about 10 μ.

S. Willdenovii Baker (fig. 95).

Sub-triangular, spore body 30–35 μ in diameter. Tri-radiate mark extends to the margin; the apical crest and the apical surface are scabrid. The ab-apical hemisphere is covered by a thin membrane thrown into folds, supported by struts and assuming a pseudo-reticulate form; the membrane projects beyond the spore margin about 10 μ.

The spores of this species are described by Hooker and Greville (1833, I, tab. 57) and by Hieronymous (1901, 372).

Group IV. GROUP OF S. SCANDENS.

The spores of this group are distinguished by the presence of a well-marked annular ring, varying in width from 5 to 10 μ; the outline of the ring may be smooth and entire, or uneven and notched or crenate. The spore size ranges from 25 to 40 μ.

Key to the Species.

A. Outline of annular ring entire.	
B. Apical surface granular	*S. puberula*, fig. 98
BB. ,, ,, warty	*S. scandens*, fig. 99
AA. Outline of annular ring notched.	
B. Ring 5 μ with a crenate margin	*S. Parkeri*, fig. 101
BB. ,, 7–10 μ with a notched margin	*S. stellata*, fig. 100

S. Parkeri Spring (figs. 101 *a* and *b*).

Tetrahedral, almost spherical, spores 25–35 μ in diameter. Tri-radiate mark extending to the margin; the apical crest is irregularly toothed. The exospore on both apical and ab-apical surfaces is ornamented with coarse, warty processes. The annular ring is 5 μ in thickness and has a crenate edge.

The spores of this species are mentioned by Spring (1849, p. 226) and Hieronymous (1901, 407).

S. puberula Spring (figs. 98 *a* and *b*).

Tetrahedral, almost spherical, spores 30–35 μ in diameter. Tri-radiate mark extending to the margin; apical surface finely granular. The ab-apical hemisphere bears irregular, warty processes. The annular ring is 7–10 μ in thickness and with a smooth entire outline.

The spores of this species are mentioned by Hieronymous (1901, 392).

S. scandens Spring (figs. 99 *a* and *b*).

Tetrahedral, almost spherical, spores 35–40 μ in diameter. Tri-radiate mark extending to the margin. The exospore has a rugose and warty surface. The annular ring, 5–7 μ in thickness, is smooth in outline.

The spores of this species are described by Spring (1849, p. 192) and Hieronymous (1901, 391).

S. stellata Spring (figs. 100 *a* and *b*).

Tetrahedral, sub-triangular, spores 25–30 μ in diameter. Tri-radiate mark extending to the margin; apical crest with a conspicuous toothed ridge; apical surface studded with small spinose processes. The ab-apical hemisphere bears large, 5 μ, blunt, warty elevations. The annular ring is unevenly notched and 7–10 μ in thickness.

The spores of this species are described by Hieronymous (1901, 410).

Group V. GROUP OF S. FIRMULA.

Spores having a diameter of 15–40 μ; exospore smooth and without ornamentation; apical crest generally conspicuous and frequently bearing a thin, membranous flange.

Key to the Species.

A. Species with a distinct apical crest furnished with a narrow membranous flange.	
B. Spore diameter 25–30 μ.	
C. Wall 3 μ thick	*S. cordifolia*, fig. 102
CC. Wall thin, less than 2 μ	*S. firmula*, fig. 103 *S. Kurzii* *S. phanotricha*
BB. Spore diameter 30–35 μ.	
C. Wall 2 μ or more thick	*S. Christii* *S. myosuroides* *S. Springii* *S. Volkensii*, fig. 104
CC. Wall less than 2 μ in thickness . . .	*S. Hochreutineri*, fig. 106 *S. leoneensis*
AA. Species with a conspicuous apical crest, but without a well-developed flange; wall thin.	
B. Apical crest narrow.	
C. Spore diameter 15–20 μ	*S. Hartwegiana*
CC. ,, ,, 25–30 μ	*S. alutacia* *S. minutifolia* *S. Morgani* *S. nana*, fig. 107
BB. Apical crest conspicuous; tri-radiate mark in a furrow between two ridges, which tend to separate.	
C. Spore diameter 20–30 μ	*S. Roxburghii*, fig. 105 *S. sepikensis*
CC. ,, ,, 30–40 μ.	
D. Wall thin, less than 2 μ	*S. Burbidgei*, fig. 108 *S. Menziesii*
DD. Wall 3 μ	*S. marginata*, fig. 109

S. alutacia Spring

Tetrahedral, sub-triangular, spores 25–30 μ in diameter. Wall thin. Tri-radiate mark extends to the margin; apical crest conspicuous. Exospore smooth.

The spores of this species are mentioned by Spring (1849, p. 237) and Hieronymous (1901, 287).

S. Burbidgei Baker (fig. 108).

Tetrahedral, sub-triangular, spores 30–35 μ in diameter. Wall thin. Tri-radiate mark extends to the margin, and is situated in a furrow between two ridges which have a tendency to separate; apical crest conspicuous. Exospore smooth.

The spores of this species are mentioned by Hieronymous (1901, 251).

S. Christii Hieron.

Tetrahedral, sub-triangular, spores 25–35 μ in diameter. Wall 2 μ in thickness. Tri-radiate mark extends to the margin; apical crest prominent and bearing a distinct flange. Exospore smooth.

S. cordifolia Spring (fig. 102).

Tetrahedral, sub-triangular, spores, 25–30 μ. Wall 3 μ in thickness. Tri-radiate mark extends to the margin; apical crest prominent and bearing a pronounced flange. Exospore smooth.

The spores of this species are mentioned by Spring (1849, p. 103) and Hieronymous (1901, 168).

S. firmula A. Br. (fig. 103).

Tetrahedral, sub-triangular, spores 25–30 μ in diameter. Wall thin. Tri-radiate mark extends to the margin; apical crest prominent and bearing a distinct flange. Exospore smooth.

The spores of this species are mentioned by Hieronymous (1901, 84).

S. Hartwegiana Spring

Tetrahedral, sub-triangular, spores 15–20 μ in diameter. Wall thin. Tri-radiate mark extends to the margin; apical crest pronounced. Exospore smooth.

The spores of this species are mentioned by Hieronymous (1901, 80).

S. Hochreutineri Hieron. (fig. 106).

Tetrahedral, sub-triangular, spores 30–35 μ in diameter. Wall thin. Tri-radiate mark extends to the margin; apical crest conspicuous and bearing a distinct flange. Exospore smooth.

S. Kurzii Baker

Tetrahedral, sub-triangular, spores 25–30 μ in diameter. Wall thin. Tri-radiate mark extending to the margin; apical crest conspicuous, bearing a distinct flange. Exospore smooth.

The spores of this species are mentioned by Hieronymous (1901, 310).

S. leoneensis Hieron.

Tetrahedral, sub-triangular, spores 30–35 μ in diameter. Wall thin. Tri-radiate mark extends to the margin; apical crest conspicuous and bearing a flange. Exospore smooth.

The spores of this species are mentioned by Hieronymous (1901, 293).

S. marginata Spring (fig. 109).

Tetrahedral, sub-triangular, spores 35 μ in diameter. Wall 3 μ in thickness. Tri-radiate mark extends to the margin and is situated in a furrow between ridges; the apical crest is conspicuous. Exospore smooth.

S. Menziesii Spring

Tetrahedral, sub-triangular, spores 30–35 μ in diameter. Wall thin. Tri-radiate mark extends to the margin, situated in a furrow; apical crest prominent. Exospore smooth.

The spores of this species are described by Hooker and Greville (1831, II, tab. 200), Spring (1849, p. 185), Hieronymous (1901, 81), Skottsberg (1942), who considers this a variety of *S. arbuscula*, and figured by Knox (1938, fig. 10).

S. Morgani Zeiller

Tetrahedral, sub-triangular, spores 25–30 μ in diameter. Wall thin. Tri-radiate mark extends almost to the margin; apical crest pronounced. Exospore smooth.

S. myosuroides (Kaulf.) Spring

Tetrahedral, sub-triangular, spores 30–35 μ in diameter. Wall 2 μ. Tri-radiate mark extends to the margin; apical crest prominent and bearing a flange. Exospore smooth.

The spores of this species are described by Kaulfuss (1824, p. 19), Brackenridge (1854, p. 339), Spring (1849, p. 236) and Hieronymous (1901, 157).

S. nana (Desv.) Spring (fig. 107).

Tetrahedral, sub-triangular, spores 25-30 μ in diameter. Tri-radiate mark extends to the margin; apical crest conspicuous, but without a flange. Exospore smooth.

The spores of this species are mentioned by Brackenridge (1854, p. 336).

S. phanotricha Baker

Tetrahedral, sub-triangular, spores 25–30 μ in diameter. Wall thin. Tri-radiate mark extends to the margin; apical crest well developed and bearing a distinct flange. Exospore smooth.

The spores of this species are mentioned by Hieronymous (1901, 282).

S. Roxburghii (Hk. & Gr.) Spring (fig. 105).

Tetrahedral, sub-triangular, spores 20 μ in diameter. Wall thin. Tri-radiate mark extends to the margin; situated in a furrow between two ridges; apical crest conspicuous. Exospore smooth.

S. sepikensis Hieron.

Tetrahedral, sub-triangular, spores 20–30 μ in diameter. Wall thin. Tri-radiate mark extends to the margin, situated in a furrow between two ridges; apical crest conspicuous. Exospore smooth.

S. Springii Gaudich.

Tetrahedral, sub-triangular, spores 30–35 μ in diameter. Wall 2 μ in thickness. Tri-radiate mark extends to the margin: apical crest conspicuous and bounded by a flange. Exospore smooth.

The spores of this species are mentioned by Hieronymous (1901, 82).

S. Volkensii Hieron. (fig. 104).

Tetrahedral, sub-triangular, spores 30–35 μ in diameter. Wall 2 μ in thickness. Tri-radiate mark extends to the margin; apical crest well developed and bearing a distinct flange. Exospore smooth.

Group VI. GROUP OF S. HELVETICA.

Spores measuring 20–40 μ in diameter; exospore granular; apical crest well developed and may bear a membranous flange.

Key to the Species.

A. Wall 2 μ in thickness.	
B. Tri-radiate crest with a flange . . .	*S. Whitmeei*, fig. 110
BB. Tri-radiate crest without a flange.	
C. Tri-radiate mark situated in a furrow . .	*S. helvetica*, fig. 111 *S. intertexta*
CC. Tri-radiate mark with a conspicuous crest .	*S. Kernbachii*, fig. 112
AA. Wall thin, less than 2 μ in thickness.	
B. Tri-radiate crest with a flange . . .	*S. philippina*, fig. 113 *S. reticulata* S. *Vaupelii*
BB. Tri-radiate crest without a flange, but with a conspicuous ridge.	
C. Exospore coarsely granular.	
D. Spore diameter 20–25 μ	*S. megaphylla*, fig. 114 *S. ramosissima*
DD. ,, ,, 30–35 μ	*S. amphirrhizos*
CC. Exospore finely granular	*S. arbuscula*, fig. 115 *S. Martensii* *S. Reineckii* *S. revoluta* *S. usta*

S. amphirrhizos A. Br.

Tetrahedral, sub-triangular, 30–35 μ. Wall thin. Tri-radiate crest conspicuous, extending to the margin. Exospore coarsely granular, as in the spores of *S. megaphylla* (fig. 114).

The spores of this species are mentioned by Hieronymous (1901, 379).

S. arbuscula Spring (fig. 115).

Tetrahedral, sub-triangular, 25–35 μ. Wall thin. Tri-radiate crest well developed and extending to the margin. Exospore smooth to faintly granular.

The spores of this species are mentioned by several authors: Kaulfuss (1824, p. 20), Hooker and Greville (1831, II. tab. 200), Spring (1849, p. 183), Brackenridge (1854, p. 333), Hillebrand (1888, p. 648), Hieronymous (1901, 76), Brown and Brown (1931, p. 112), Selling (1946, p. 20, figs. 22, 23).

S. helvetica Link (fig. 111).

Tetrahedral, sub-triangular, 35–40 μ. Wall 2 μ thick. Tri-radiate mark conspicuous, and situated in a narrow furrow bounded on either side by thin ridges and extending almost to the margin. Exospore faintly granular.

The spores of this species are described and figured by Hieronymous (1901, fig. 405) and Hegi (1936, fig. 15).

S. intertexta Spring

Tetrahedral, sub-triangular, 30–40 μ. Wall 2 μ in thickness. Tri-radiate mark conspicuous and situated in a furrow bounded by narrow ridges, and extending almost to the margin. Exospore smooth to finely granular. The spores of this species are very similar to those of *S. helvetica* (fig. 111).

S. Kernbachii Hieron. (fig. 112).

Tetrahedral, sub-triangular, 30 35 μ. Wall 2 μ in thickness. Tri-radiate crest conspicuous and extending to the margin. Exospore granular.

The spores of this species are mentioned by Hieronymous (1901, 335).

S. Martensii Spring

Tetrahedral, sub-triangular, 25–30 μ. Wall thin. Tri-radiate mark conspicuous and extending to the margin. Exospore granular.

The spores of this species are mentioned by Hieronymous (1901, 217).

S. megaphylla Baker (fig. 114).

Tetrahedral, sub-triangular, 20–25 μ. Wall thin. Tri-radiate mark conspicuous and extending to the margin. Exospore granular.

The spores of this species are described by Hieronymous (1901, 239).

S. philippina Spring (fig. 113).

Tetrahedral, sub-triangular, 30–35 μ. Wall thin. Tri-radiate mark conspicuous with a well-developed flange and extending almost to the margin. Exospore smooth to faintly granular.

S. ramosissima Baker

Tetrahedral, sub-triangular, 20–25 μ. Wall thin. Tri-radiate mark 2/3 radius, with a conspicuous crest. Exospore coarsely granular.

S. Reineckei Hieron.

Tetrahedral, sub-triangular, 25–35 μ. Wall thin. Tri-radiate mark extending to the margin with a well-developed crest, particularly prominent at the angles. Exospore faintly granular.

The spores of this species are mentioned by Hieronymous (1901, 83).

S. reticulata (Hk. & Gr.) Spring

Tetrahedral, sub-triangular, 30–40 μ. Wall thin. Tri-radiate mark conspicuous with a well-developed flange and extending to the margin. Exospore smooth to slightly rough or granular.

S. revoluta Baker

Tetrahedral, sub-triangular, 25–30 μ. Wall thin. Tri-radiate crest conspicuous and extending to the margin. Exospore finely granular as in the spores of *S. helvetica* (fig. 111).

S. usta Vieill.

Tetrahedral, sub-triangular, 30–35 μ. Wall thin. Tri-radiate mark conspicuous and extending to the margin. Exospore finely granular.

The spores of this species are mentioned by Hieronymous (1901, 334).

S. Vaupelii Hieron.

Tetrahedral, sub-triangular, 30–35 μ. Wall thin. Tri-radiate crest with a distinct flange and extending to the margin. Exospore granular.

S. Whitmeei Baker (fig. 110).

Tetrahedral, sub-triangular, 30–35 μ. Wall 2 μ in thickness.

Tri-radiate mark with a conspicuous flange and extending to the margin. Exospore finely granular.

The spores of this species are mentioned by Hieronymous (1901, 88).

Group VII. Group of S. cathedrifolia.

Spores, except in *S. tamariscina*, mostly small, 20–35 μ in diameter. Exospore rugose and papillate. The margin of the spore is more or less crenulate.

Key to the Species.

A. Spores large, 60–70 μ	*S. tamariscina*, fig. 116
AA. Spore diameter less than 35 μ.	
B. Spore diameter 20–25 μ.	
C. Apical crest conspicuous	*S. cathedrifolia*, fig. 117
CC. ,, ,, inconspicuous	*S. producta*, fig. 118
BB. Spore diameter 25–35 μ.	
C. Spore diameter 30–35 μ	*S. heterostachys*, fig. 119
CC. ,, ,, 25–30 μ.	
D. Apical crest conspicuous.	
E. Exospore papillate	*S. concinna* *S. deliquescens* *S. falcata*, fig. 120
EE. Exospore finely papillate	*S. Savatieri*, fig. 121
D.D Apical crest inconspicuous	*S. platybasis*, fig. 122

S. cathedrifolia Spring (figs. 117 *a* and *b*).

Tetrahedral, sub-triangular, 20–25 μ. Wall 1–2 μ in thickness. Tri-radiate crest conspicuous and extending almost to the margin. Exospore papillate; margin of spore crenulate.

S. concinna A. Br.

Tetrahedral, sub-triangular, 25–30 μ. Wall 1–2 μ in thickness. Tri-radiate crest well developed and extending to the margin. Exospore rough and papillate; the sculpturing resembles that in the spores of *S. cathedrifolia* (fig. 117).

The spores of this species are mentioned by Hieronymous (1901, 384); they are figured by Knox (1938, fig. 15).

S. deliquescens Spring

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extends to the margin and has a prominent apical crest. Exospore rugose and papillate; margin crenulate. The sculpturing of the spores of this species is similar to that of the spores of *S. falcata* (fig. 120).

The spores of this species are mentioned by Hieronymous (1901, 389).

S. falcata Spring (fig. 120).

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. Apical crest well developed. Exospore rugose and papillate; margin crenulate.

The spores of this species are mentioned by Hieronymous (1901, 390).

S. heterostachys Baker (fig. 119).

Tetrahedral, sub-triangular, 30–35 μ. Wall 2 μ in thickness. Tri-radiate mark extending to the margin. Exospore rugose and papillate; margin crenulate.

S. platybasis Baker (fig. 122).

Tetrahedral, sub-triangular, 25–30 μ. Wall thin. Tri-radiate mark extending to the margin. Exospore rugose and papillate; margin crenulate.

The spores of this species are mentioned by Hieronymous (1901, 213).

S. producta Baker (fig. 118).

Tetrahedral, sub-triangular, 20 μ. Wall thin. Tri-radiate mark extending to the margin. Exospore rugose and papillate; margin crenulate.

The spores of this species are mentioned by Hieronymous (1901, 255).

S. Savatieri Baker (fig. 121).

Tetrahedral, sub-triangular, 25–30 μ. Wall thin. Tri-radiate mark extending almost to the margin; apical crest well developed. Exospore finely papillate; margin minutely crenulate.

S. tamariscina (Beauv.) Spring (fig. 116).

Spores spherical, 60–70 μ. Tri-radiate mark 1/2 radius. Exospore rugose, irregularly and coarsely papillate; margin crenulate.

The spores of this species are mentioned by Spring (1849, p. 64) and Hieronymous (1901, 62).

Group VIII. Group of S. radicata.

Spores measuring 20–45 μ in diameter; ornamented with low, irregularly shaped, warty elevations, varying in breadth from 2 to 5 μ and usually set 2–5 μ apart. The elevations are seen on the spore margin which is crenate.

Key to the Species.

A. Spore diameter 20–30 μ.	
B. Spore diameter 20–25 μ	*S. Kittyae*
BB. ,, ,, 25–30 μ.	
C. Apical crest conspicuous	*S. apus*, fig. 123 *S. Ludoviciana*, fig. 124 *S. caudata*
CC. ,, ,, not conspicuous	*S. velutina*, fig. 125
AA. Spore diameter 30–45 μ.	
B. Apical surface papillate.	
C. Spore diameter 30–40 μ	*S. dendricola* *S. d'Urvillaei*
CC. ,, ,, 40–45 μ	*S. pallidissima*, fig. 126
BB. Apical surface warty, not papillate.	
C. Apical crest conspicuous	*S. aristata* *S. Balfouri*, fig. 127
CC. ,, ,, not conspicuous	*S. abyssinica*, fig. 128 *S. carnea* *S. latupana* *S. radicata*, fig. 129 *S. sub-diaphana*, fig. 130 *S. tenera*, fig. 131 *S. tetragonostachya*

S. abyssinica Spring (fig. 128).

Tetrahedral, sub-triangular, 30–40 μ. Tri-radiate mark extending to the margin. Exospore ornamented with low, irregular, warty elevations about 2–5 μ across and set 2 μ apart; spore margin crenate.

The spores of this species are described by Hieronymous (1901, 158).

S. apus Spring (figs. 123 *a* and *b*).

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin, and possessing a well-developed crest. Exospore bears low, irregular, warty processes. Spore margin crenate.

The spores of this species are mentioned by Hieronymous (1901, 257) and figured by Lyon (1901, fig. 69).

S. aristata Spring

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin, possessing a well-developed crest. Exospore with low, irregular, warty processes, 2 μ broad and closely set together.

S. Balfouri Baker (fig. 127).

Tetrahedral sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin, apical crest prominent. Exospore ornamented on all sides with low, irregular, rounded processes about 2-4 μ broad and set 1–2 μ apart; spore margin crenate.

The spores of this species are mentioned by Hieronymous (1901, 385).

S. carnea vA. vR.

Tetrahedral, sub-triangular, 30–40 μ. Tri-radiate mark extending to the margin, apical crest conspicuous. Exospore rugose, with irregular, low, uneven ridges. Spore margin crenate.

S. caudata (Desv.) Spring

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin, apical crest conspicuous. Exospore rugose with low, irregular, warty processes; margin crenate.

The spores of this species are mentioned by Hieronymous (1901, 346).

S. dendricola Jenman

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with low, irregular, warty processes, 2–5 μ broad, becoming smaller towards the apical crest, and closely set together; spore margin crenate.

S. d'Urvillaei (Bory) Al. Br.

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with low, irregular, warty processes, 2–4 μ broad, closely set together, becoming smaller towards the apical crest.

The spores of this species are mentioned by Hieronymous (1901, 368).

S. Kittyae vA. vR.

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. Exospore rugose, with low, irregular, warty processes; spore margin crenate.

S. latupana vA. vR.

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with low, irregular, warty processes, 2 μ broad and set 2 μ apart.

S. Ludoviciana A. Br. (fig. 124).

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin, apical crest conspicuous. Exospore rugose, with a rough warty surface; spore margin crenate.

The spores of this species are mentioned by Hieronymous (1901, 256).

S. pallidissima Spring (fig. 126).

Tetrahedral, sub-triangular, 40–45 μ. Tri-radiate mark extending almost to the margin. Exospore ornamented with low, irregular, warty processes, 2–4 μ broad on the ab-apical side, becoming papillate towards the apical crest; spore margin crenate.

The spores of this species are described by Spring (1849, p. 234) and Hieronymous (1901, 176).

S. radicata (Hk. & Gr.) Spring (fig. 129).

Tetrahedral, sub-triangular, 35–40 μ. Tri-radiate mark extending to the margin. Exospore ornamented with low, irregular, warty processes, 2–4 μ broad and set 2 μ apart; spore margin crenate.

The spores of this species are described by Spring (1849, p. 114) and Hieronymous (1901, 173).

S. sub-diaphana (Wall.) Spring (fig. 130).

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending almost to the margin. Exospore rough, with low, irregular, warty processes.

S. tenera (Hk. & Gr.) Spring (fig. 131).

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore bears low, irregular, warty processes, 2 μ broad and closely set together; spore margin crenate.

The spores of this species are described by Spring (1849, p. 241) and Hieronymous (1901, 313).

S. tetragonostachya Wall.

Tetrahedral, sub-triangular, 30–40 μ. Tri-radiate mark extending to the margin. Exospore ornamented with low, irregular, warty processes, 2 μ broad and very closely set together; spore margin crenate.

S. velutina Cesati (fig. 125).

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. Exospore bears low, irregular, warty processes, 2 μ broad and closely set together.

Group IX. Group of S. leptophylla.

Spores measuring 25–45 μ; studded with small, low, rounded processes, 1–2 μ long and arranged regularly 1–3 μ apart.

Key to the Species.

A. Processes 2 μ in length.	
B. Spore diameter 25–35 μ	*S. pentagona*, fig. 132
BB. ,, ,, 35–45 μ	*S. effusa*, fig. 133
AA. Processes 1 μ in length, spore size 30–35 μ	*S. Bodinieri* *S. boninensis* *S. ciliaris*, fig. 134 *S. leptophylla*, fig. 135

S. Bodinieri Hieron.

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore studded with small rounded processes, 1 × 1 μ, and closely set together.

S. boninensis Baker

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore studded with small rounded processes, 1 × 1 μ, closely set, about 2–3 μ apart.

S. ciliaris (Retz.) Spring (fig. 134).

Tetrahedral, sub-triangular to round, 30–35 μ. Tri-radiate mark extending to the margin. Exospore studded with short, 1 μ, blunt processes, set about 2–3 μ apart.

The spores of this species are described by Spring (1849, p. 233), Brackenridge (1854, p. 337) and Hieronymous (1901, 175).

S. effusa Alston (fig. 133).

Tetrahedral, sub-triangular, 35–45 μ. Tri-radiate mark extending to the margin. Exospore studded with small blunt processes, 2 μ long and set 1–3 μ apart.

S. leptophylla Baker (fig. 135).

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with small, low, 1 μ, rounded elevations, regularly arranged 2–3 μ apart. The processes are seen on the edge of the spore and give it a crenate outline.

S. pentagona Spring (fig. 132).

Tetrahedral, sub-triangular, 25–35 μ. Tri-radiate mark extending to the margin. Exospore studded with small, rounded processes, 2 × 2 μ, and closely set together.

The spores of this species are described by Spring (1849, p. 150) and Hieronymous (1901, 112).

Group X. Group of S. vaginata.

Spores measuring from 25 to 50 μ in diameter; ornamented with irregularly shaped, rounded elevations, ranging from 3 to 8 μ in breadth and variously spaced. The spore margin is uneven and sinuate.

Key to the Species.

A. Spore diameter 40–50 μ . . . . . . *S. Mettenii*, fig. 136
AA. ,, ,, 25–40 μ.
  B. Spore size 25–30 μ . . . . . *S. tenuifolia*, fig. 137

BB. Spore size 30–40 μ	*S. Hewithii* *S. involvens* *S. mongholica* *S. opaca*, fig. 138 *S. sinensis*, fig. 139 *S. sub-cordata* *S. vaginata*, fig. 140 *S. yemensis*

S. Hewithii Hieron.

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore bears irregular, warty processes, 5–8 μ in diameter, close together and becoming smaller towards the apical crest; spore margin uneven, sinuate.

S. involvens (Sw.) Spring

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore studded with irregular, warty processes, varying in diameter from 3 to 7 μ, closely set together; spore margin sinuate.

S. Mettenii A. Br. (fig. 136).

Tetrahedral, sub-triangular, 40–50 μ. Tri-radiate mark extending almost to the margin. Exospore ornamented with large, irregularly shaped bosses, 3–8 μ across, becoming smaller around the apical crest.

S. mongholica Ruprecht

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with large, rounded tuberculate processes, 5–8 μ broad, closely set together and most conspicuous on the ab-apical surface.

The spores of this species are described by Hieronymous (1901, 49) and figured by Knox (1938, fig. 17). This species is probably synonymous with *S. sinensis* (Desv.) Spring (fig. 139).

S. opaca Warb. (fig. 138).

Tetrahedral, sub-triangular, 30–40 μ. Tri-radiate mark extending to the margin. Exospore ornamented with large, warty processes closely set together; on the ab-apical side the processes measure 3–7 μ in diameter, and towards the apical crest become smaller; spore margin sinuate.

The spores of this species are described by Hieronymous (1901, 248).

S. sinensis (Desv.) Spring (fig. 139).

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with large, rounded tuberculate processes, 3–7 μ broad; spore margin sinuate.

S. sub-cordata A. Br.

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with large tuberculate bosses, 3–7 μ broad, closely set together. The apical surface is less heavily ornamented than the ab-apical.

S. tenuifolia Spring (fig. 137).

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. Exospore ornamented with irregular, tuberculate bosses, varying in diameter from 3 to 6 μ and closely set together; spore margin sinuate. The apical surface is rough and with indifferent sculpturing.

The spores of this species are mentioned by Spring (1849, p. 253).

S. vaginata Spring (figs. 140 *a* and *b*).

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with large, irregularly shaped warty processes. On the ab-apical side the tubercles are 3–5 μ across, while on the apical surface they become small and towards the apical crest are papillate. The spore margin is sinuate.

The spores of this species are mentioned by Spring (1849, p. 87).

S. yemensis Spring

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears large, irregular warty processes, 3–5 μ across; round the apical crest the surface is papillate to almost smooth.

The spores of this species are described by Spring (1849, p. 193) and Hieronymous (1901, 50).

Group XI. GROUP OF S. REPANDA.

Spores measuring from 25 to 55 μ in diameter; ornamented with conspicuous irregularly shaped flattened bosses, varying in diameter from 3 to 10 μ, and separated from one another by winding channels. The spore margin is uneven and sinuate.

Key to the Species.

A. Spore diameter 25–35 μ; elevations 3–8 μ in breadth	*S. Beccariana*, fig. 141 *S. duriuscula*
AA. Spore diameter 35–55 μ; elevations 5–10 μ in breadth.	
B. Spore diameter 30–35 μ	*S. calcicola*, fig. 142
BB. ,, ,, 35–55 μ; elevations smaller towards apex.	
C. Spore diameter 35–40 μ	*S. d'Armandvillei*
CC. ,, ,, 50–55 μ	*S. repanda*, fig. 143

S. Beccariana Baker (fig. 141).

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. Exospore rough, with large, irregular, warty elevations varying in diameter from 3 to 7 μ and separated by winding channels; spore margin sinuate.

S. calcicola Hieron. (fig. 142).

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin situated in a furrow. Exospore ornamented on all surfaces with large, irregular, warty elevations, 5–8 μ in diameter, separated by winding channels; spore margin sinuate.

S. d'Armandvillei vA. vR.

Tetrahedral, sub-triangular, 35–40 μ. Tri-radiate mark extending to the margin. Exospore closely covered on the ab-apical surface with large, warty elevations, 5–7 μ broad, separated by winding channels. Towards the apical crest the processes become smaller.

S. duriuscula Alston

Tetrahedral, sub-triangular, 25–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with irregular, warty elevations varying in diameter from 3 to 8 μ, close together and separated by winding channels. Round the apical crest the processes are smaller and scattered; spore margin sinuate.

S. repanda (Desv.) Spring (figs. 143 *a* and *b*).

Tetrahedral, sub-triangular, 50–55 μ. Tri-radiate mark extending to the margin. Exospore ornamented with large, flat, irregularly shaped elevations, 5–10 μ in breadth, and separated from one another by winding channels. On the apical surface the processes are smaller; the spore margin is sinuate.

Group XII. Group of S. stolonifera.

Spores measuring 20–40 μ. Ornamentation of blunt, straight-sided, rod-like processes, 1–2 μ in thickness and varying in length from 2 to 5 μ. The processes in most species are regularly arranged, either densely packed or set from 3 to 5 μ apart.

Key to the Species.

A. Processes short, less than 3 μ long and spaced 3–5 μ apart.	
B. Spore diameter 20–25 μ.	
C. Processes broad at base	*S. Hookeri*, fig. 144
CC. „ thin „ „	*S. monospora*, fig. 145
BB. Spore diameter 25–35 μ	*S. finium* *S. permutata*, fig. 146 *S. polystachya*, fig. 147

AA. Processes more than 3 μ long and densely packed.
B. Spore diameter 20–30 μ . . . . . *S. delicatula*
S. picta
BB. ,, ,, 25–40 μ.
C. Spore diameter 25–35 μ . . . . . *S. exaltata*
S. inaequalifolia, fig. 148
S. pennata
S. stipulata
S. stolonifera, fig. 149
CC. ,, ,, 30–40 μ . . . . . *S. conferta*, fig. 150
S. fulvicaulis
S. Vogelii

S. conferta Baker (fig. 150).

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore studded with short, blunt processes, 3–5 μ long and closely set together, 2–3 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 166).

S. delicatula (Desv.) Alston

Tetrahedral, sub-triangular, 20–30 μ. Tri-radiate mark extending to the margin. Exospore studded with blunt, rod-like processes, 5 μ long and set 2 μ apart.

S. exaltata (Kze.) Spring

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented on all faces with blunt, rod-like processes, 3–4 μ long and set 2–4 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 412).

S. finium vA. vR.

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. On the ab-apical surface the exospore bears blunt processes, 3 μ long and set 3–5 μ apart; round the apical crest the sculpturing is papillate.

S. fulvicaulis Hieron.

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. Exospore studded with blunt processes, 3 μ long and set 2–3 μ apart. On the apical surface the sculpturing is papillate.

S. Hookeri Baker (fig. 144).

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. Exospore ornamented with short, blunt, tuberculate processes, 2 μ long and set 3 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 144).

S. inaequalifolia (Hk. & Gr.) Spring (fig. 148).

Tetrahedral, sub-triangular, 25–35 μ. Tri-radiate mark extending to the margin. Exospore on all faces bears blunt processes, 3–5 μ in length and set closely 2–3 μ apart.

The spores of this species are described by Hieronymous (1901, 350).

S. monospora Spring (fig. 145).

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. Exospore studded with blunt processes, 3 μ long, very evenly disposed on all surfaces, 3 μ apart.

The spores of this species are described by Spring (1849, p. 135) and by Hieronymous (1901, 236).

S. pennata (Don) Spring

Tetrahedral, sub-triangular to almost spherical, 25–35 μ. Tri-radiate mark extending to the margin. Exospore studded with short, blunt processes, 2–3 μ in length and set 2–3 μ apart.

S. permutata Hieron. (fig. 146).

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. Exospore bears short, blunt processes, 2–3 μ long and set 3–5 μ apart.

S. picta A. Br.

Tetrahedral, sub-triangular to spherical, 20–35 μ. Tri-radiate mark extending to the margin. Exospore studded with blunt, rod-like processes, 3–4 μ long and set 2–3 μ apart.

The spores of this species are described by Hieronymous (1901, 349) and figured by Knox (1938, fig. 19).

S. polystachya (Warb.) Hieron. (fig. 147).

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. Exospore ornamented with thin, blunt processes, 2–3 μ long and set 3–5 μ apart.

The spores of this species are described by Hieronymous (1901, 362).

S. stipulata (Bl.) Spring

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. Exospore studded with blunt processes, 2–3 μ long and closely set 2–3 μ apart.

S. stolonifera Spring (fig. 149).

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. Exospore studded with blunt, rod-like processes, 2–3 μ in length and regularly disposed 2 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 404).

S. Vogelii Spring

Tetrahedral, sub-triangular, 30–40 μ. Tri-radiate mark extending to the margin. Exospore ornamented with blunt, rod-like processes, 3–5 μ in length and set 3 μ apart.

The spores of this species are described by Spring (1849, p. 170) and Hieronymous (1901, 72).

Group XIII. Group of S. biformis.

Spores measuring 15–35 μ; ornamented with blunt, straight-sided rod-like processes, 1–2 μ in thickness and varying in length from 2 to 5 μ. The processes are few in number and widely spaced, in most species more than 5 μ apart.

Key to the Species.

A. Processes short, 3 μ or less in length.	
B. Spore diameter 15–20 μ	*S. Griffithii*
	S. intermedia, fig. 151
BB. ,, ,, more than 20 μ.	
C. Spore diameter 20–25 μ	*S. Burkei*
	S. caulescens, fig. 152
	S. haematodes, fig. 153
	S. Jagorii
	S. Leveriana
	S. viticulosa
CC. ,, ,, 25–35 μ	*S. ascendens*, fig. 154
	S. umbrosa
AA. Processes more than 3 μ in length, usually 5 μ.	
B. Spore diameter 15–20 μ	*S. aenea*
	S. frondosa, fig. 155
	S. poperangensis
BB. ,, ,, more than 20 μ.	
C. Spore diameter 20–25 μ	*S. bahiensis*
	S. biformis, fig. 156
	S. cupra
	S. jungermannioides
	S. Möllendorffii
	S. Muelleri
	S. Neei
	S. novae-guineae
	S. pallida
	S. Paxii
	S. pulcherrima
CC. ,, ,, 25–30 μ	*S. Ramosii*
	S. serpens
	S. trachyphylla, fig. 157

S. aenea Warb.

Tetrahedral, sub-triangular, 15–20 μ. Tri-radiate mark extending to the margin. Exospore on the ab-apical side ornamented with thin, straight-sided, blunt processes, 5 μ long and spaced 5–8 μ apart.

S. ascendens vA. vR. (fig. 154).

Tetrahedral, sub-triangular to spherical, 30–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented on the ab-apical surface with thin, blunt processes, 3 μ in length and widely spaced 5–7 μ apart.

S. bahiensis Spring

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. Exospore on the ab-apical side ornamented with thin, blunt processes, 5 μ long and spaced 3–5 μ apart.

S. biformis A. Br. (fig. 156).

Tetrahedral, sub-triangular to spherical, 20–25 μ. Tri-radiate mark extending to the margin. Exospore studded with thin, blunt processes, 3–5 μ long and spaced 3–7 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 99).

S. Burkei Hieron.

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. Exospore on the ab-apical side bears thin, blunt processes, 3 μ in length and spaced 5 μ apart. The apical surface is devoid of ornamentation.

S. caulescens (Wall.) Spring (fig. 152).

Tetrahedral, sub-triangular to spherical, 25 μ. Tri-radiate mark extending to the margin. Exospore bears short, blunt processes, 2 μ in length and set 5 μ apart.

The spores of this species are described by Spring (1849, p. 158) and Hieronymous (1901, 89).

S. cupra Riel.

Tetrahedral, sub-triangular to spherical, 20–25 μ. Tri-radiate mark extending to the margin. Exospore on the ab-apical surface bears thin, stick-like processes, 5 μ long and spaced 5–8 μ apart. The apical surface is without ornamentation.

S. frondosa Warb. (fig. 155).

Tetrahedral, sub-triangular to spherical, 15–20 μ. Tri-radiate mark extending to the margin. Exospore ornamented on the ab-apical side with blunt processes, 5 μ long and widely spaced 8–10 μ apart. The apical surface is without ornamentation.

The spores of this species are described by Hieronymous (1901, 108).

S. Griffithii Spring

Tetrahedral, sub-triangular to spherical, 15–20 μ. Tri-radiate mark extending to the margin. Exospore on the ab-apical side studded with short, blunt processes, 3 μ long and set 3–5 μ apart.

The spores of this species are described by Hieronymous (1901, 100).

S. haematodes Spring (fig. 153).

Tetrahedral, sub-triangular, 20 μ. Tri-radiate mark extending to the margin. Exospore on the ab-apical side bears short, blunt processes, 2 μ long and set 5–7 μ apart. The apical surface is unornamented.

The spores of this species are described by Hieronymous (1901, 125).

S. intermedia (Bl.) Spring (fig. 151).

Tetrahedral, sub-triangular, 15–20 μ. Tri-radiate mark extending to the margin. Exospore on the ab-apical surface bears short blunt processes, 2–3 μ long and spaced 5 μ apart.

S. Jagorii Warb.

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. Exospore on the ab-apical side bears short, blunt processes, 3 μ long and spaced 5–7 μ apart. The apical surface is without ornamentation.

The spores of this species are described by Hieronymous (1901, 97).

S. jungermannioides Spring

Tetrahedral, sub-triangular to spherical, 25 μ. Tri-radiate mark extending to the margin. Exospore studded with stick-like processes, about 5 μ in length and 3–5 μ apart on the ab-apical side. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 203).

S. Leveriana Alston

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. Exospore studded with short, blunt processes, 2 μ long and widely spaced 5–8 μ apart.

S. Möllendorffii Hieron.

Tetrahedral, sub-triangular to spherical, 25 μ. Tri-radiate mark extending to the margin. Exospore studded with blunt, stick-like processes, 3–5 μ in length and set 5–7 μ apart.

The spores of this species are described by Hieronymous (1901, 102).

S. Muelleri Baker

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. Exospore ornamented with blunt, stick-like processes, 3–5 μ long and 5 μ or more apart on the ab-apical side. The apical surface is without sculpturing.

S. Neei Hieron.

Tetrahedral, sub-triangular to spherical, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears thin, blunt processes, 5 μ in length and set 5 μ or more apart.

S. novae-guineae Hieron.

Tetrahedral, sub-triangular to spherical, 25 μ. Tri-radiate mark extending to the margin. Exospore bears thin, blunt processes, 3–5 μ long and set 5 μ apart.

The spores of this species are described by Hieronymous (1901, 119).

S. pallida Spring

Tetrahedral, sub-triangular to spherical, 25 μ. Tri-radiate mark extending to the margin. Exospore on the ab-apical side bears blunt processes, 3–5 μ long and set 5–8 μ apart. The apical side is without ornamentation.

The spores of this species are mentioned by Spring (1849, p, 116).

S. Paxii Hieron.

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. On the ab-apical surface the exospore bears thin, stick-like blunt processes, 5 μ long and spaced 5–8 μ apart.

S. poperangensis Hieron.

Tetrahedral, sub-triangular to spherical, 20 μ. Tri-radiate mark extending to the margin. Exospore studded with blunt processes, 5 μ long and set 5–6 μ apart. The apical surface is devoid of ornamentation.

S. pulcherrima Liebm.

Tetrahedral, sub-triangular to spherical, 25 μ. Tri-radiate mark extending to the margin. Exospore studded with blunt processes, 3–5 μ long and spaced 5–8 μ apart.

The spores of this species are described by Hieronymous (1901, 98).

S. Ramosii Hieron.

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. Exospore studded with blunt processes, 3–5 μ long and set 5–7 μ apart.

S. serpens Spring

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. Exospore studded with straight, rod-like processes, 5 μ long and set 5–8 μ apart.

The spores of this species are mentioned by Spring (1849, p. 102) and Hieronymous (1901, 206); they are figured by Knox (1938, fig. 11).

S. trachyphylla A. Br. (fig. 157).

Tetrahedral, sub-triangular, 28–30 μ. Tri-radiate mark extending to the margin. Exospore ornamented with blunt rod-like processes, 3–5 μ long on the ab-apical side and set 3–5 μ apart. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 229).

S. umbrosa Lemaire

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears short, blunt processes, 3 μ long and set 3–5 μ apart. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 124).

S. viticulosa Klotzsch

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. Exospore, on the ab-apical side, studded with short, blunt processes, 2 μ long and set 3–5 μ apart. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 128).

Group XIV. Group of S. latifrons.

Spores measuring from 15 to 30 μ in diameter; the basal hemisphere furnished with thin, straight, blunt, rather widely spaced, rod-like processes, 5–10 μ in length and from 3 to 8 μ apart. The apical hemisphere is without ornamentation.

Key to the Species.

A. Spore diameter 15–20 μ.	
B. Processes 8–10 μ in length	*S. sumatrana*, fig. 159
BB. „ 5–8 μ „ „	*S. atroviridis*, fig. 158 *S. breynioides* *S. luzonensis*
AA. Spore diameter 20–30 μ.	
B. Spore diameter 20–25 μ; processes set 3–6 μ apart	*S. longipinna*, fig. 160 *S. trifurcata* *S. regularis*
BB. Spore diameter 25–30 μ; processes set 5–8 μ apart.	
C. Processes 5 μ in length	*S. latifrons*, fig. 161 *S. Swartzii*
CC. „ more than 5 μ in length . .	*S. denudata*, fig. 162 *S. halconensis* *S. rhodospora*

S. atroviridis Spring (fig. 158).

Tetrahedral, sub-triangular, 15–20 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears long, thin, rod-like outgrowths, 5–8 μ in length and set 5–8 μ apart. The apical hemisphere is without ornamentation.

A description of the species is given by Hooker and Greville (1837, I, tab. 39) under the name *Lycopodium atroviridis*.

S. breynioides Baker

Tetrahedral, sub-triangular, 15–20 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is studded with thin, rod-like processes 5 μ long and set 5–7 μ apart. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 86).

S. denudata Spring (fig. 162).

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is studded with rod-like processes, 5–7 μ long and set 5–7 μ apart. Around the apical crest the ornamentation is absent.

S. halconensis Hieron.

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. Exospore, on the ab-apical side, furnished with rod-like processes, 5–7 μ long and set 5–8 μ apart. The apical surface is without ornamentation.

S. latifrons Warb. (fig. 161).

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. Exospore on the ab-apical side bears blunt, rod-like processes, 5 μ long and set 5–6 μ apart. The apical surface is without ornamentation.

The spores of this species are described by Hieronymous (1901, 115).

S. longipinna Warb.

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears thin, rod-like processes, 5 μ long and spaced 3–5 μ apart. The apical surface is without ornamentation.

The spores of this species are described by Hieronymous (1901, 107).

S. luzonensis Hieron.

Tetrahedral, sub-triangular, 15–20 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is furnished with rod-like processes, 5 μ long and set 5–8 μ apart. The apical surface is without ornamentation.

The spores of this species are described by Hieronymous (1901, 113, and 1902).

S. regularis Baker

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears thin, blunt processes, 5–8 μ long and set 3–5 μ apart. The apical surface is without ornamentation.

S. rhodospora Baker

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears thin, rod-like processes, 5–8 μ long and set 5–10 μ apart. The apical surface is without ornamentation.

S. sumatrana Hieron. (fig. 159).

Tetrahedral, sub-triangular, 15–20 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears rod-like processes, 8–10 μ long and set 5–8 μ apart. The apical surface is without ornamentation.

S. Swartzii Spring

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears rod-like processes, 5 μ long and set 5–6 μ apart. The apical surface is without ornamentation.

S. trifurcata Baker

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is furnished with thin, rod-like processes, 5 μ long and set 3–6 μ apart. The apical surface is without ornamentation.

Group XV. GROUP OF S. SUB-ARBORESCENS.

Spores measuring 15–35 μ in diameter; rather sparsely furnished with stout, conical emergences appearing as broad-based spines from 2 to 5 μ in length and in most species 2 μ broad at the base; the processes are spaced 2–8 μ distant from one another. The apical surface is free from ornamentation.

Key to the Species.

A. Spores 15–20 μ in diameter	*S. Breynii*
	S. Jouani
	S. sub-arborescens, fig. 163
	S. versicolor
AA. „ 20–35 μ in diameter.	
B. Spore diameter 20–25 μ.	
C. Processes 2–3 μ, widely spaced 5–8 μ apart .	*S. augustiramea*
	S. confusa
	S. Elmeri, fig. 164
	S. Rolandi-principis
CC. Processes 3–5 μ, spaced 5 μ apart . .	*S. cupressina*, fig. 165
BB. Spore diameter 25–36 μ.	
C. Spore diameter 30–35 μ	*S. erectifolia*, fig. 166
	Lycopodium densum, fig. 75
CC. „ „ 25–30 μ	*S. calosticha*
	S. Davidei
	S. Fénixii
	S. Kochii
	S. peltata, fig. 167
	S. Plumieri
	S. truncata
	S. Weberbaueri

S. augustiramea Muell. and Bak.

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is studded with short, conical elevations 2 μ high and set 5–8 μ apart. The apical surface is without ornamentation.

S. Breynii Spring

Tetrahedral, sub-triangular, 15–20 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears short conical processes, 3 μ long and set 3–5 μ apart. The apical surface is without ornamentation.

The spores of this species are recorded by Spring (1849, p. 119) and Hieronymous (1901, 210).

S. calosticha Spring

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears short, conical processes, set 2–5 μ apart. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 209).

S. cupressina A. Br. (fig. 165).

Tetrahedral, sub-triangular, 20 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is furnished with thin, pointed processes, 3–5 μ long and set 3–6 μ apart. The apical surface is without ornamentation.

The spores of this species are mentioned by Spring (1849, p. 113), Brackenridge (1854, p. 337) and Hieronymous (1901, 104).

S. Davidei Franchet

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears stout, conical processes, up to 5 μ in length and set 3–6 μ apart. The apical surface is without ornamentation.

S. Elmeri Hieron. (fig. 164).

Tetrahedral, sub-triangular, 20–30 μ. Tri-radiate mark extending to the margin. The exospore on the ab-apical side studded with conical processes, 3 μ long and set 5–8 μ apart. The apical surface is without ornamentation.

S. erectifolia Spring (fig. 166).

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. The apical surface is devoid of ornamentation, and the exospore on the ab-apical side is studded with stout, conical processes, 5 μ in length and 2 μ broad at the base, set 5–8 μ apart.

S. Fénixii Hieron.

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. The exospore bears conical processes 3–4 μ long and set 3–5 μ apart on the ab-apical side; round the apical crest the surface is smooth or papillate.

S. Jouani Hieron.

Tetrahedral, sub-triangular, 15–20 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears conical processes, 3–4 μ long and set 3–5 μ apart. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 110).

S. Kochii Hieron.

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears stout, conical processes, 3 μ long and set 3–5 μ apart. The apical surface is without ornamentation.

S. peltata Presl. (fig. 167).

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. On the ab-apical surface the exospore bears stout, conical processes, 2 μ long and set 5–8 μ apart. The apical surface is without ornamentation.

S. Plumieri Hieron.

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is studded with short, stout, conical processes, 3 μ long and set 3–5 μ apart. The apical surface is without ornamentation.

S. Rolandi-principis Alston

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. The exospore is studded with short, stout, conical processes, 2–3 μ long and set 5–8 μ apart. The apical surface is without ornamentation.

S. sub-arborescens Hook. (figs. 163 *a* and *b*).

Tetrahedral, sub-triangular, 15–20 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is studded with short, stout, conical processes, 2–3 μ long and set 3–5 μ apart. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 406).

S. truncata A. Br.

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears stout, conical processes, 2 μ long and set 2–3 μ apart. The apical surface is without ornamentation.

The spores of this species are described by Hieronymous (1901, 205).

S. versicolor Spring

Tetrahedral, sub-triangular, 15–20 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears short, stout, conical processes, 2–3 μ long and set 3–5 μ apart. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 155).

S. Weberbaueri Hieron.

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears stout, conical processes, 3–4 μ long and set 3–5 μ apart. The apical surface is without ornamentation.

Group XVI. Group of S. anceps.

Spores measuring 20–35 μ in diameter, ornamented with short. conical, pointed emergences, densely packed together. The processes are small, from 1 to 3 μ in length, and set 2–5 μ apart.

Key to the Species.

A. Spore diameter 30–35 μ	*S. Wallichii*, fig. 168
AA. ,, ,, 20–30 μ.	
B. Processes acicular	*S. anceps*, fig. 169 *S. erythropus*, fig. 170
BB. ,, stout and conical	*S. blepharostachys*, fig. 171 *S. Mayerhoffii*, fig. 172

S. anceps Presl. (fig. 169).

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears minute acicular processes, 1–2 μ long and set 2–3 μ apart; the spore margin has a denticulate appearance. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 105).

S. blepharostachys Alston (figs. 171 *a* and *b*).

Tetrahedral, sub-triangular, 20–30 μ. Tri-radiate mark extending to the margin; apical crest conspicuous. The exospore is ornamented with small, conical, spinose processes, 2 μ long, numerous and closely set, 2 μ apart. On the apical side the emergences are sparse and absent from the apical crest.

S. erythropus (Mart.) Spring (fig. 170).

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is ornamented with fine acicular processes, 2–3 μ long and set 3–5 μ apart. The apical surface is without emergences.

The spores of this species are described by Hieronymous (1901, 123).

S. Mayerhoffii Hieron. (fig. 172).

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears stout, conical processes, 2 μ long and set 3–5 μ apart. The apical surface is without ornamentation.

S. Wallichii Spring (fig. 168).

Tetrahedral, sub-triangular to spherical, 30–35 μ. Tri-radiate mark extending to the margin. Exospore bears short, stout, conical processes, 2 μ long, sometimes coalescing at the base, closely arranged 2–3 μ apart.

The spores of this species are described by Hieronymous (1901, 357).

Group XVII. Group of S. uncinata.

Spores measuring 20–35 μ in diameter; furnished with long spinose processes, densely packed together. The spines vary in length from 4 to 7 μ and have a base of 1–3 μ broad; the spines are irregularly arranged and spaced 2–5 μ apart.

Key to the Species.

A. Spinose processes long, up to 7 μ.	
B. Spines stout, with a base 3 μ broad . .	*S. Eggersii*, fig. 173 *S. eurynota* *S. intacta*, fig. 174 *S. lingulata* *S. polycephala* *S. pubescens*
BB. Spines thin, with a narrow base.	
C. Spore diameter 20–25 μ	*S. articulata*, fig. 175 *S. bombycina*, fig. 176 *S. caudorhiza*
CC. ,, ,, 25–35 μ	*S. epirrhizos* *S. horizontalis* *S. Lindigii* *S. mnioides* *S. uncinata*, fig. 177
AA. Spinose processes less than 5 μ.	
B. Spore diameter 20–25 μ	*S. chilensis*, fig. 178 *S. geniculata*, fig. 179
BB. ,, ,, 25–35 μ	*S. Galeottei* *S. Poeppigiana*, fig. 180 *S. sulcata* *S. trisulcata*

S. articulata Spring (fig. 175).

Tetrahedral, sub-triangular to spherical, 20–25 μ. Tri-radiate mark extending to margin. Exospore bears spinose processes on all faces; on the ab-apical side they are long, up to 7 μ, set 3–4 μ apart. Those on the apical side are shorter.

The spores of this species are mentioned by Hieronymous (1901, 427).

S. bombycina Spring (fig. 176).

Tetrahedral, sub-triangular to spherical, 20–30 μ. Tri-radiate mark extending to the margin. Exospore densely covered with sharp spines, 4–6 μ long, and about 3 μ apart on the ab-apical side; on the apical surface the processes are shorter.

The spores of this species are mentioned by Spring (1849, p. 191).

S. caudorhiza Baker

Tetrahedral, sub-triangular to spherical, 20–30 μ. Tri-radiate mark extending to the margin. Exospore ornamented on all faces with sharp, spinose processes, 5–7 μ long and densely set together, 3–5 μ apart.

S. chilensis Spring (fig. 178).

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. Exospore ornamented on all faces with sharp spines up to 5 μ in length, and irregularly arranged about 3 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 365).

S. Eggersii Sodiro (fig. 173).

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. The exospore bears stout, spinose processes, 7 μ long and 3 μ broad at the base; they are densely packed together, set about 3 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 433).

S. epirrhizos Spring

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is ornamented with sharp, spinose processes, 5–8 μ long and 2 μ at base, densely packed 3–5 μ apart. Round the apical crest the spines are shorter and less densely arranged.

The spores of this species are mentioned by Hieronymous (1901, 426).

S. eurynota A. Br.

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. Exospore covered with stout spines, 5–8 μ long, 3 μ broad at the base, and densely packed together 3–5 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 414).

S. Galeottei Spring

Tetrahedral, sub-triangular to spherical, 25 35 μ. Tri-radiate mark extending to the margin. The exospore is ornamented with sharp spines about 5 μ in length and set 3–5 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 435) and figured by Knox (1938, fig. 13).

S. geniculata Spring (fig. 179).

Tetrahedral, sub-triangular, 20–30 μ. Tri-radiate mark extending to the margin. Exospore ornamented on all faces with sharp spines 5 μ long and set 3–5 μ apart.

The spores of this species are described by Spring (1849, p. 227) and Hieronymous (1901, 441).

S. horizontalis (Presl.) Spring

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented on all faces with sharp spines 5–7 μ long and set 3–5 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 415).

S. intacta Baker (fig. 174).

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. The exospore is ornamented with stout, spinose processes, 7 μ long, 3 μ broad at the base, and densely set 3–5 μ apart. On the apical side the processes are short and less closely packed.

The spores of this species are mentioned by Hieronymous (1901, 398).

S. Lindigii A. Br.

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. The exospore is ornamented with spinose processes, 5–7 μ long, closely packed together 3–5 μ apart. Round the apical crest the spines are short and scattered.

The spores of this species are mentioned by Hieronymous (1901, 432).

S. lingulata Spring

Tetrahedral, sub-triangular, 25–35 μ. Tri-radiate mark extending to the margin. Exospore on the ab-apical side studded with stout spines, 7 μ long and 3 μ broad at the base; spines arranged irregularly about 5 μ apart. On the apical surface the spines are short and scattered.

The spores of this species are mentioned by Hieronymous (1901, 424).

S. mnioides A. Br.

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is ornamented with sharp spinose processes, 7 μ long, and closely packed together 2–4 μ apart. On the apical surface the spines are short and scattered.

The spores of this species are mentioned by Hieronymous (1901, 436).

S. Poeppigiana Spring (fig. 180).

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. Exospore is ornamented with sharp spines 5 μ long, densely packed together 2–4 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 423).

S. polycephala Baker

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears stout spinose processes, 7 μ long and 3 μ broad at the base; the processes are set 3–5 μ apart. On the apical surface the spines are small and scattered.

S. pubescens (Wall.) Spring

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with stout, spinose processes, 7 μ long and 3 μ broad at the base; the spines are irregularly arranged and set 2–4 μ apart.

The spores of this species are described by Spring (1849, p. 173) and Hieronymous (1901, 73).

S. sulcata Spring

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. Exospore bears sharp, spinose processes, 5 μ long, irregularly disposed 2–4 μ apart.

The spores of this species are mentioned by Spring (1849, p. 214) and Hieronymous (1901, 413).

S. trisulcata Aspl.

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with sharp spines 5 μ long and set 3–5 μ apart.

S. uncinata Spring (figs. 177 *a* and *b*).

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. Exospore bears spinose processes, 5–7 μ long and set 3–4 μ apart. On the apical side the spines are smaller and scattered.

The spores of this species are described by Hieronymous (1901, 341).

Group XVIII. GROUP OF S. MAGNIFICA.

Spores measuring 20–35 μ in diameter; ornamented on the ab-apical hemisphere with slender, pointed, acicular processes, widely spaced. The acicles vary in length from 3 to 8 μ, and are regularly arranged from 5 to 10 μ apart. The apical surface is smooth.

Key to the Species.

A. Acicular processes less than 5 μ in length . .	*S. cagayanensis*, fig. 181 *S. longissima* *S. pilosula*
AA. ,, ,, 5 μ or more in length.	
B. Acicles thin and up to 8 μ long.	
C. Spore diameter 20–25 μ	*S. Spanielema*, fig. 182 *S. speciosa*
CC. ,, ,, 25–35 μ	*S. Brooksii*, fig. 183 *S. contigua* *S. tomentosa*
BB. Acicles 5 μ long.	
C. Spore diameter 20–25 μ	*S. alopecuroides* *S. Keistingii* *S. latifolia* *S. magnifica*, fig. 184 *S. Wariensis*
CC. ,, ,, 25–35 μ	*S. alligans*, fig. 185 *S. ambigua* *S. Copelandii* *S. flabellata*

S. alligans Hieron. (fig. 185).

Tetrahedral, sub-triangular, 25–35 μ. Tri-radiate mark extending to the margin. Exospore ornamented with sharp, acicular processes, 5 μ long and 5–10 μ apart. On the apical surface the acicles are absent.

S. alopecuroides Baker

Tetrahedral, sub-triangular to spherical, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears thin, acicular processes, 3–5 μ long and 5 μ apart. The apical surface is smooth.

The spores of this species are described by Hieronymous (1901, 231).

S. ambigua A. Br.

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears acicular processes, 5 μ long and set 5–10 μ apart. The apical surface is smooth.

The spores of this species are mentioned by Hieronymous (1901, 165).

S. Brooksii Hieron. (fig. 183).

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is ornamented with thin, acicular processes, 5–7 μ long, sometimes curved and set 5–6 μ apart. The apical surface is smooth.

S. cagayanensis Hieron. (fig. 181).

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears fine, acicular processes, 3 μ long and widely spaced 5–10 μ apart. The apical surface is smooth.

S. contigua Baker

Tetrahedral, sub-triangular, 30–35 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears acicular spines, 5–7 μ long and set 5–10 μ apart. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 234).

S. Copelandii Hieron.

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears thin, acicular spines, 5 μ long and set 5–8 μ apart. The apical surface is without ornamentation.

S. flabellata Spring

Tetrahedral, sub-triangular, 25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears acicular processes, 5 μ long and set 5–8 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 130).

S. Keistingii Hieron.

Tetrahedral, sub-triangular, 20 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears acicular processes, 5 μ long and set 5–8 μ apart. The apical surface is without ornamentation.

S. latifolia Spring

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears fine acicular processes, 5 μ long and set 5–8 μ apart. The apical surface is smooth.

The spores of this species are described by Spring (1849, p. 168) and Hieronymous (1901, 141).

S. longissima Baker

Tetrahedral, sub-triangular, 25–30 μ. Tri-radiate mark extending to the margin. Exospore bears acicular processes, 3 μ long and set 3–5 μ apart. On the apical surface the acicles are few and scattered.

The spores of this species are mentioned by Hieronymous (1901, 497).

S. magnifica Warb. (fig. 184).

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is ornamented with fine acicular processes, 5 μ long and set 5–8 μ apart. On the apical surface the processes are absent.

The spores of this species are mentioned by Hieronymous (1901, 137).

S. pilosula vA. vR.

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. The exospore is ornamented with fine, acicular processes, 3–5 μ long and set 5 μ apart. On the apical surface the acicles are absent.

S. Spanielema Alston (fig. 182).

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears acicular processes, up to 8 μ long and set 5–8 μ apart. The apical surface is without ornamentation.

S. speciosa A. Br.

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore is ornamented with fine acicular processes, 5–7 μ long and set 5 μ apart. The apical surface is smooth.

The spores of this species are mentioned by Hieronymous (1901, 138).

S. tomentosa Spring

Tetrahedral, sub-triangular to spherical, 25–30 μ. Tri-radiate mark extending to the margin. The exospore bears long, acicular processes, 5–7 μ and set 5 μ apart. The apical surface is without ornamentation.

The spores of this species are mentioned by Hieronymous (1901, 442).

S. Wariensis Hieron.

Tetrahedral, sub-triangular, 20–25 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears short, acicular processes, 5 μ long and set 5 μ apart. The apical surface is without ornamentation.

Group XIX. GROUP OF S. SELAGINOIDES.

Spores measuring 25–40 μ in diameter; furnished with stout, coarse, conical processes having a spreading base 5 μ broad. The spines vary in length from 5 to 12 μ, tapering to a point and arranged irregularly and widely spaced.

Key to the Species.

A. Processes set more than 10 μ apart . . . *S. selaginoides*, fig. 186
AA. „ „ less „ 10 μ „ . . . *S. atirrensis*, fig. 187

S. atirrensis Hieron. (fig. 187).

Tetrahedral, sub-triangular to spherical, 25–35 μ. Tri-radiate mark extending to the margin. Apical surface papillate. Exospore on ab-apical side studded with coarse spinose processes, 3 μ broad at the base, with blunt or straight ends, about 5–8 μ long, irregularly arranged and widely spaced 5–8 μ apart.

The spores of this species are mentioned by Hieronymous (1901, 438).

S. selaginoides (L.) Link (figs. 186 *a* and *b*).

Tetrahedral, sub-triangular to spherical, 35–40 μ. Tri-radiate mark extending to the margin, apical crest prominent. On the ab-apical surface the exospore is ornamented with coarse, stout, blunt spinose processes, 5–8 μ long, spreading at the base to 5 μ, and widely spaced 10–15 μ apart. The apical surface is finely granular.

The microspores of this familiar species are described by several authors: Link (1842), Milde (1859), Braun (1860), Luerssen (1889), Hieronymous (1901, fig. 401), Hegi (1936, taf. I, fig. 51), Reeve (1935, Pl. 380), Erdtman (1943, figs. 487, 488).

Group XX. GROUP OF S. KRAUSSIANA.

Spores measuring 30–55 μ in diameter; furnished with long, stout, curved spines. The spines measure up to 12 μ in length, and have a base varying from 3 to 7 μ and are irregularly arranged.

Key to the Species.

A. Spines widely spaced . . . . . . *S. Kraussiana*, fig. 188
AA. „ closely „ . . . . . . *S. Kunzeana*, fig. 189

S. Kraussiana A. Br. (fig. 188).

Tetrahedral, sub-triangular to spherical, 50-55 μ. Tri-radiate mark 2 3 radius and frequently seen to be open. On the ab-apical side the exospore bears long, stout, curved spines, up to 12 μ long and widely spaced 10 μ or more apart. Surrounding the apical slit the spines are short and broad at the base.

The spores of this species are mentioned by Hieronymous (1901, 420) and are figured by Slagg (1932, Pl. V).

S. Kunzeana A. Br. (fig. 189).

Tetrahedral, sub-triangular to spherical, 30–50 μ. Tri-radiate mark extending to the margin. On the ab-apical side the exospore bears stout, curved spines 8–12 μ long, with a spreading base up to 7 μ broad. The spines are closely set on the ab-apical surface, but on the apical side they are short and scattered.

The spores of this species are mentioned by Hieronymous (1901, 429).

SPORE STRUCTURE IN SELAGINELLACEAE.

The genus Selaginella comprises some 600 species, and of these about 350 have been examined, representative of all the sub-genera and series as formulated by Walton and Alston (1938).

The microspores are relatively small, usually ranging from 15 to 50 μ, but a few may measure up to 60 μ in diameter. This is in contrast to the spores of the genus Lycopodium, where they are most frequently 40–50 μ in diameter.

The spore shape throughout the genus Selaginella is sphaericotetrahedral. The ornamentation usually takes the form of protuberances or outgrowths of the wall, which are of three main types, the spinose, tuberculate and rod-like. All may be regarded as having been derived from a smooth-walled form as seen in *S. firmula* (fig. 103), slight deviations from which are illustrated in the granular appearance of *S. helvetica* (fig. 111) or the finely papillate form of *S. cathedrifolia* (fig. 117). An increasing degree of spinosity is observed in such species as *S. sub-arborescens* (fig. 163), *S. uncinata* (fig. 177) and *S. Kraussiana* (fig. 188); a series with acicular outgrowths is exemplified in *S. cagayanensis* (fig. 181), *S. magnifica* (fig. 184) and *S. Spanielema* (fig. 182), in the latter of which the acicles attain a length of 8 μ. The tuberculate type includes spores whose walls have rounded, warty elevations as in *S. radicata* (fig. 129); where the excrescences become more pronounced the coarsely tuberculate type is reached as in *S. vaginata* (fig. 140) and *S. sinensis* (fig. 139). The third series comprises spores characterised by the presence of thin, parallel-sided, rod-like outgrowths as seen in *S. stolonifera* (fig. 149), *S. biformis* (fig. 156), *S. latifrons* (fig. 161), culminating in *S. sumatrana* (fig. 159) with the processes 10 μ in length.

In addition to the three more common types referred to, some species of Selaginella are distinguished by the possession of a membranous outgrowth; this membrane may encircle the entire spore body as in *S. sibirica* (fig. 77), or may be confined to the ab-apical hemisphere as wing-like outgrowths, supported by strengthening struts as seen in *S. megastachya* (fig. 96) and *S. integerrima* (fig. 92), or be reduced to an equatorial flange as in *S. sanguinolenta* (fig. 86).

Finally, a type, infrequent in occurrence, is distinguished by the presence of an annular equatorial ring as seen in *S. scandens* (fig. 99).

No single type of sculpturing has been found to be characteristic of any one of the four sub-genera of Selaginella, as defined by Walton and Alston, nor of any single series within a sub-genus. Thus it cannot be maintained that the spore sculpturing accords with the classification in Selaginella, and, in fact, there is no noticeable relationship between spore morphology and any of the taxonomic arrangements suggested. This is in contrast to the genus Lycopodium, where the spore morphology has been shown to bear some relationship to classification, if only in a general way. In neither genus, however, can any connection be traced between spore morphology and ecological conditions.

It can, however, be stated that the spores of Selaginella, so far examined by the author or described by Hieronymous (1901), differ materially in sculpturing and external morphology from those of Lycopodium, and the spores of the two genera would not be likely to be confused with one another. Whereas in Lycopodium the exospore is pitted or reticulate, in Selaginella the ornamentation exhibits some form of outgrowth from the spore wall, either in the form of spines, tuberculate processes, or a membranous wing; no such excrescences are featured amongst the spores of Lycopodium, with the one exception of *L. densum* (fig. 75).

ISOETACEAE.

General Characters and Classification.

The family *Isoetaccae* comprises three genera: Isoetes, with over 60 species, and the fossil genera Nathorstiana and Pleuromeia. The family is characterised by a short, erect axis with crowded acicular leaves, all of which may be fertile. The base of the axis forms a swollen meristem which produces dichotomously forked roots in regular succession.

Members of the genus Isoetes are relatively small, herbaceous plants, occupying diverse habitats. Some are essentially lacustrine, submersed in water, others are xerophytic forms occurring on dry hillsides. They are inhabitants chiefly of cool, climatic regions, rare or absent in the tropics. All the leaves may be fertile, and the plants are heterosporous.

The name was first mentioned by Linnaeus in 1751, and two years later he established the genus. Delile, in 1827, was the first to give a detailed account of the development of Isoetes, based on an examination of *I. setacea*. Interest in the genus was further stimulated through the work of Braun (1864), and by 1867 Milde was able to refer to 15 species. A synopsis of the genus was published by Baker in 1880, which was later incorporated in his Fern Allies (1887). In this synopsis 46 species are brought together, and the primary divisions of the genus are based upon the geographical distribution of the species. Following Baker's work, Motelay and Vendryès (1883) published a monograph of the genus. They recognised 47 species and give figures of several spore forms. Other systematic accounts dealing mainly with N. American forms were published, but no outstanding addition to our knowledge of the genus was made until 1922, when Pfeiffer published her "Monograph of the Isoetaceae". This work contains a useful account of the history, morphology and ecological relationships of Isoetes, together with a classification based upon the sculpturing of the megaspores. Recently, Williams (1943) published a morphological account of a new species from Western Australia.

Pfeiffer recognises four sections, *Tuberculatae*, *Echinatae*, *Cristatae* and *Reticulatae*, characterised by megaspores possessing tuberculate, spiny, crested or reticulate exospores respectively. Sixty-four species are described in detail, and in the majority of cases mention is made of the microspores, though these have not been found to be of much diagnostic value.

The present account describes the microspores of 40 species of Isoetes. Following the procedure adopted in *Lycopodiaceae* and *Selaginellaceae*, the microspores are segregated into groups having similar spore ornamentation. On this basis three groups of microspore types are recognised: Group I, in which the exospore is smooth or granular; Group II, with papillate ornamentation; Group III, with setose exospore. A key is given to the groups as well as keys to series of species within each group. The number after references to Pfeiffer (1922) is that which she has given to the particular species under review.

Genus I. ISOETES.

Key to Groups.

A. Exospore smooth to finely granular; margin entire	I. Group echinospora
AA. Exospore rugose, papillate or setose; margin not entire.	
B. Exospore rugose or papillate	II. Group adspersa
BB. Exospore setose	III. Group Hystrix

Group I. Group of I. echinospora.

Spores ovoid, 25–40 μ in length, about 20 μ in breadth. The exospore is smooth to granular; margin entire.

In this group there are few distinguishing characters; the spores vary little in size and, being practically devoid of sculpturing, they are difficult to distinguish from one another.

Key to the Species.

A. Spore length more than 30 μ	*I. Drummondii*, fig. 190 *I. Pringlei* *I. riparia* *I. Savatieri*

AA. Spore length usually about 30 μ . . . *I. boliviensis*
I. echinospora, fig. 191
I. Ekmani
I. lacustris
I. mexicana
I. Piperi
I. saccharata
I. setacea
I. Tuckermani
AAA. „ „ less than 30 μ . . . . *I. foveolata*
I. Howellii
I. Tuerckheimii

I. boliviensis Weber

Spores 30 × 20 μ. Ovoid in outline. Exospore smooth to finely granular; margin entire.

No mention of the spores of this species has been found in the literature.

I. Drummondii A. Br. (figs. 190 *a* and *b*).

Spores 30–35 × 20 μ. Ovoid in outline with a well-developed apical crest. Exospore coarsely granular; margin entire.

The spores of this species are described by Motelay and Vendryès (1883) and by Pfeiffer (1922, 20).

I. echinospora Dur. (figs. 191 *a* and *b*).

Spores 30 × 20 μ. Ovoid in outline. Exospore smooth to granular; margin entire.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 40); they are figured by Erdtman (1943, figs. 454–457).

I. Ekmani Weber

Spores 30 × 20 μ. Ovoid in outline. Exospore smooth to granular; margin entire.

No mention of the spores of this species has been found in the literature.

I. foveolata var. *plenospora* Eaton

Spores 25–30 × 20 μ. Ovoid in outline with a well-developed apical ridge. Exospore granular; margin entire.

The spores of this species are described by Pfeiffer (1922, 56).

I. Howellii Engelm.

Spores 25–30 × 20 μ. Ovoid in outline with a well-developed apical crest. Exospore smooth to faintly granular; margin entire.

The spores of this species are described by Pfeiffer (1922, 34).

I. lacustris L.

Spores 30 × 20 μ. Ovoid in outline. Exospore almost smooth; margin entire.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887), Pfeiffer (1922, 51) and Erdtman (1943, fig. 458).

I. mexicana Und.

Spores 30 × 20 μ. Ovoid in outline with a well-developed apical ridge. Exospore smooth to granular; margin entire.

The spores of this species are described by Pfeiffer (1922, 37).

I. Piperi Eaton

Spores 30 × 20 μ. Ovoid in outline. Exospore faintly granular; margin entire.

The spores of this species are described by Pfeiffer (1922, 53).

I. Pringlei Und.

Spores 35 × 25 μ. Ovoid in outline with a well-developed apical crest. Exospore granular; margin entire.

The spores of this species are described by Pfeiffer (1922, 49).

I. riparia Engelm.

Spores 30–35 × 20–25 μ. Ovoid in outline. Exospore smooth to granular; margin entire.

The spores of this species are described by Motelay and Vendryès (1883) and by Pfeiffer (1922, 48).

I. saccharata var. *Amesii* Eaton

Spores 30 × 15 μ. Ovoid in outline. Exospore smooth to finely granular; margin entire.

The spores of this species are described by Pfeiffer (1922, 47).

I. Savatieri Franchet

Spores 30–40 × 20–25 μ. Ovoid in outline with a well-developed apical crest. Exospore granular; margin entire.

The spores of this species are described by Motelay and Vendryès (1883) and by Pfeiffer (1922, 45).

I. setacea Bosc.

Spores 30 × 20 μ. Ovoid in outline. Exospore granular; margin entire.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 6).

I. Tuckermani A. Br.

Spores 30 × 20 μ. Ovoid in outline. Exospore granular to rugose; margin entire.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 55).

I. Tuerckheimii Brause

Spores 25–30 × 15–20 μ. Ovoid in outline. Exospore smooth to minutely papillate; margin entire.

The spores of this species are described by Pfeiffer (1922, 36).

Group II. GROUP OF I. ADSPERSA.

Spores ovoid, measuring 20–40 μ in length and 15–20 μ in breadth. The exospore is papillate or faintly reticulate with an uneven margin, usually crenulate.

Key to the Species.

A. Spores more than 30 μ in length.	
B. Exospore faintly reticulate	*I. ovata*, fig. 192
BB. ,, papillate	*I. amazonica* *I. azorica* *I. Gardneriana*, fig. 193
AA. Spores about 30 μ in length; exospore papillate .	*I. adspersa*, fig. 194 *I. Braunii* *I. Schweinfurthii*
AAA. Spores less than 30 μ in length	*I. capensis* *I. coromandelina* *I. flaccida* *I. Nuttallii* *I. Stephansenii*

I. adspersa A. Br. (figs. 194 *a* and *b*).

Spores measure 30 × 20 μ. Ovoid in outline with a well-developed apical crest. Exospore granular to papillate; margin finely crenulate.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 10).

I. amazonica A. Br.

Spores 30–35 × 20 μ. Ovoid in outline with a well-developed apical crest. Exospore granular to finely tuberculate; margin faintly crenulate.

The spores of this species are described by Pfeiffer (1922, 21).

I. azorica Dur.

Spores 35–40 × 20–25 μ. Ovoid in outline with a conspicuous apical ridge. Exospore papillate; margin crenulate.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 59).

I. Braunii Dur.

Spores 30 × 20 μ. Ovoid in outline. Exospore papillate; margin crenulate.

The spores of this species are described by Baker (1887) and Pfeiffer (1922, 42).

I. capensis A. Duthie

Spores 25–30 × 20 μ. Ovoid in outline with a well-developed apical ridge. Exospore rugose to papillate; margin crenulate.

No mention of the spores of this species has been found in the literature.

I. coromandelina L. fil.

Spores 20–30 × 15–20 μ. Ovoid in outline with a well-developed apical ridge. Exospore rugose to papillate; margin crenulate.

The spores of this species are described by Pfeiffer (1922, 5).

I. flaccida Shuttlew.

Spores 20–30 × 15–20 μ. Ovoid in outline with a well-developed apical ridge. Exospore papillate; margin crenulate.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 31).

I. Gardneriana A. Br. (figs. 193 *a* and *b*).

Spores 30–35 × 20–25 μ. Ovoid in outline with a conspicuous apical ridge. Exospore rugose to papillate; margin crenulate.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 22).

I. Nuttallii A. Br.

Spores 25–30 × 15–20. μ Ovoid in outline with a well-developed apical ridge. Exospore papillate; margin crenulate.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 26).

I. ovata Pfeiffer (figs. 192 *a* and *b*).

Spores 30–35 × 20 μ. Ovoid in outline. Exospore lightly reticulate with ridges spine-like in silhouette; margin finely crenulate.

The spores of this species are described by Pfeiffer (1922, 3, 5).

I. Schweinfurthii A. Br.

Spores 30 × 20 μ. Ovoid in outline. Exospore minutely papillate; margin finely crenulate.

The spores of this species are described by Pfeiffer (1922, 3).

I. Stephansenii A. Duthie

Spores 25–30 × 15–20 μ. Ovoid in outline. Exospore papillose; margin crenulate.

No mention of the spores of this species has been found in the literature.

Group III. GROUP OF I. HYSTRIX.

Spores ovoid, measuring 20–40 μ in length and 15–25 μ in breadth. The exospore is ornamented with fine, setose processes, varying in length from 2 to 5 μ and set about 3–5 μ apart. The apical crest is well developed in all species.

Key to the Species.

A. Setae more than 3 μ in length.	
B. Spores more than 30 μ in length . . .	*I. habbemensis*, fig. 195 *I. stellenborisiensis* *I. Stuartii*
BB. „ 30 μ or less in length	*I. alpina* *I. Hookeri* *I. Hystrix*, fig. 197 *I. Lechleri*
AA. Setae less than 3 μ in length.	
B. Spores 30 μ in length	*I. Boetica* *I. velata*
BB. „ less than 30 μ in length	*I. Boryana* *I. japonica*, fig. 196 *I. tenuissima*

I. alpina Kirk

Spores 25–30 × 15–20 μ. Ovoid in outline with conspicuous ridges. Exospore bears stout bristles, 3–5 μ long and spaced about 5 μ apart.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 17).

I. Boetica Willk.

Spores 30 × 20 μ. Ovoid in outline with well-developed apical crest. Exospore minutely setose; setae 2–3 μ long and 3–5 μ apart.

No mention of the spores of this species has been found in the literature.

I. Boryana Dur.

Spores 20–25 × 15 μ. Ovoid in outline with conspicuous apical ridge. Exospore setose; setae 2 μ long and about 3–5 μ apart.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 11).

I. habbemensis Alston (fig. 195).

Spores 35–40 × 20–25 μ. Ovoid in outline with well-developed apical ridge. Exospore echinate; ornamentation of fine stiff bristles 5 μ long and 5 μ apart.

The spores of this species have been described by Alston (1945 *a*).

I. Hookeri A. Br.

Spores 30 × 20 μ. Ovoid in outline with well-developed apical ridge. Exospore finely setose; setae 3–4 μ long and 3–4 μ apart.

The spores of this species are described by Motelay and Vendryès (1883) and by Pfeiffer (1922, 28).

I. Hystrix Bory & Dur. (figs. 197 *a* and *b*).

Spores 30 × 20 μ. Ovoid in outline with well-developed apical ridge. Exospore echinate; ornamented with spinules 3–4 μ long and about 5 μ apart.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 25).

I. japonica A. Br. (fig. 196).

Spores 20–25 × 15 μ. Ovoid in outline with well-developed apical ridge. Exospore finely setose; bristles 2 μ long and about 5 μ apart.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 60).

I. Lechleri Mett.

Spores 35 × 20 μ. Ovoid in outline with a well-developed apical. ridge. Exospore spinulose; processes 3–5 μ long and 3–5 μ apart.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 32).

I. stellenborisiensis A. Duthie

Spore 35 × 20 μ. Ovoid in outline with well-developed apical ridge. Exospore setose; ornamentation of stout bristles 3–4 μ long and 3–5 μ apart.

No mention of the spores of this species has been found in the literature.

I. Stuartii A. Br.

Spores 30–40 × 25–30 μ. Ovoid in outline with well-developed apical ridge. Exospore setose; bristles 3 μ long, closely set about 3 μ apart.

The spores of this species are described by Baker (1887) and Pfeiffer (1922, 28).

I. tenuissima Bor.

Spores 20–25 × 20 μ. Ovoid in outline with well-developed apical ridge. Exospore setose; setae 2–3 μ long and about 3 μ apart.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 12).

I. velata A. Br.

Spores $30 \times 20\ \mu$. Ovoid in outline with well-developed apical ridge. Exospore finely setose; setae 2–3 μ long and 3–5 μ apart.

The spores of this species are described by Motelay and Vendryès (1883), by Baker (1887) and Pfeiffer (1922, 15).

Spore Structure in Isoetaceae.

The microspores of Isoetes are remarkably uniform in shape and size; they are ovoid in outline, frequently with a conspicuous apical ridge, and rarely exceed $40 \times 30\ \mu$. In the majority of species they are of small dimensions. The microspore tetrad may show bilateral or tetrahedral arrangement; the freeing of the spores, however, soon allows a change of shape and rounding of the sharp angles. The ornamentation of the exospore is granular, papillose, spinulose or setose; occasionally a wing-like extension or crest may be present on the apical side.

The three groups in which the microspore types have been arranged for present comparative purposes bear no apparent relationship to the four sections defined by Pfeiffer (1922) according to megaspore structure. Among the species which are included, for example, in Group I, in which the exospore is smooth or granular, are representatives of all four sections and types of megaspore recognised by Pfeiffer. There seems to be no correlation between type of ornamentation in the microspore and the form of sculpturing in the megaspore of the same species. Within the genus, variations in morphological characters are so small that a natural grouping of the species is a matter of difficulty. Such classifications as have been suggested are mainly useful as aids to identification. It might be argued that the microspores could be used equally as well as megaspores; their small size and the consequent difficulty of examination, however, lessens the value of microspores for systematic diagnosis; they can be of use as additional evidence, and as such they are employed very occasionally by Pfeiffer. Moreover, no obvious connection exists between the spore structure and the varied ecological conditions in which the plants live.

Of the two fossil genera, spores are known only for Pleuromeia, the microspores of which conform to the Isoetes type and are reniform in shape. Since both the fossil genera are Mesozoic members of the *Isoetaceae*, their spores, if they occur at all in the older Palaeozoic rocks, might appear only occasionally. It may be significant that similar ovoid spores have been recorded from the

Carboniferous strata, but the plants from which they originated are indeterminate.

PALAEOZOIC FOSSIL SPORES.

Following the study of the microspores of living representatives of the Lycopodiinae, an evaluation may now be made of the several characters of spore morphology most likely to be of use for specific and generic diagnosis, and suggestions advanced as to the features least subject to change and variation during geologic time, and therefore of greatest taxonomic significance.

All pteridophytic spores are formed in essentially the same manner as the result of a tetrad division of the spore mother cell; the shape of each individual member of the tetrad is either tetrahedral or bilateral, depending upon the plane of division. The scar formed at the point of attachment of a spore to other members of the tetrad is consequently either a tri-radiate or longitudinal slit. In the genera Lycopodium and Selaginella the tetrahedral form of spore is the normal one, and the tri-radiate mark is characteristic of both genera. A few unusual examples with bilateral, bean-shaped spores have been recorded for Lycopodium (Selling, 1946), but their occurrence is rare; in Isoetes, however, the microspores are ovoid in outline. The symmetry in exospore ornamentation is also influenced by the tetrad formation, though it may be slightly modified after the spores are set free from one another (Knox, 1949).

It has been shown in the preceding pages that in Lycopodium two types of exospore ornamentation only are represented, namely, the pitted and the reticulate, with the one exception of *L. densum* (fig. 75). In Selaginella and Isoetes, however, neither pitted nor conspicuously reticulate types have been noted by the present author. On the contrary, the exospore in these two genera exhibits great diversity of ornamentation in the form of outgrowth or protuberance—acicular, spinose, warty, tuberculate or rod-like, of varying length and breadth. These different types of excrescence account for the appearance of the majority of the microspores in Selaginella; the remainder have membranous extensions of the wall, which may appear as equatorial wings or as encircling bladder-like structures. It is of considerable interest that these several types of spore are all recognisable amongst microspores found in coals of Carboniferous age, but, as Schopf (1944) has pointed out, "It is important that many specific features of spores of different geologic age can be matched because of evolutionary convergence as well as because of community of derivation. Consequently, unless there exists some corroborative evidence based upon spore forms actually present in contemporaneous fossils whose relationship can be established, all that seems warranted is to direct attention to similarity of the spores of different geologic age, recognising that the similarities may or may not have phyletic implications". It is necessary, therefore, to consider briefly the record of the rocks.

Palaeozoic Plant Record.

The earliest records of land plants of which we can be reasonably certain are from rocks of Silurian age. Impressions have been found in these rocks from different parts of the world, and the records, though scanty, indicate that, by the close of the Silurian period, the invasion of the land by primitive plants had begun and thus paved the way for the evolution of a land flora.

During early Devonian times land plants show evidence of evolutionary trends along different lines. "With the discovery of the Rhynie flora and the recognition of the order *Psilophytales*, the common ancestry of all vascular plants became a matter within the bounds of proper speculation" (Darrah, 1939). The *Psilophytales*, which include the *Rhyniaceae*, are defined as dichotomous, leafless and rootless plants, with terminal homosporous sporangia. This complex group, though somewhat unnatural, provides sufficient variety in form, from which different types may be derived, and from which it is reasonable to suppose that lycopsid, sphenopsid and pteropsid lines may have evolved, though probably each along an independent path, traceable back to the algae.

Already in Middle Devonian times a habit simulating that found in Lycopodium is encountered in Asteroxylon, though the true strobiloid lycopods did not make their appearance until the Upper Devonian. During the Carboniferous period the *Lepidodendrales*, belonging to the lycopsid group, become dominant and reach a climax of development, then rapidly die out, and only a few forms persist into the Permian. Most members were arborescent, though a few were herbaceous, and show considerable diversity of form, structure and method of attachment of the cone. Five families are recognised as follows:—

I. Lepidodendraceae (Carboniferous).

The strobili (Lepidostrobus) resemble closely those of Selaginella, being ligulate but larger in proportion. Some species produced strobili with one kind of spore only, and others with both megaspores and microspores in the same cone.

II. LEPIDOCARPACEAE (Carboniferous).

Represented by one genus which bears cones with seed-like structures.

III. MIADESMIACEAE (Carboniferous).

Monotypic; a small, possibly herbaceous plant with seed-like sporophyll.

IV. BOTHRODENDRACEAE (Carboniferous).

Having the general habit of Lepidodendron, and the strobili (Bothrodendrostrobus) likewise similar to those of Selaginella.

V. SIGILLARIACEAE (Carboniferous and Permian).

Trees with unbranched axes and cones borne on special peduncles grouped in zones on the trunk and branches. Strobili heterosporous.

The only known fossil genus of the *Lycopodiaceae* is Spencerites, occurring in the Carboniferous. It bears a peltate sporophyll with a leaf-like umbo, and spores of 140 μ in diameter, with an equatorial wing (Hirmer, 1927).

Among Palaeozoic fossils there are a few herbaceous plants which in habit resemble Lycopodium or Selaginella; these are placed in the genera Lycopodites and Selaginellites respectively, the former apparently homosporous and the latter heterosporous. The presence or absence of a ligule is in most cases indeterminate, hence their assignment is uncertain.

The strobili of the extinct families were like those of living *Lycopodiales*, but in most cases of large size. Some forms were probably homosporous, but the majority were certainly heterosporous. The sporangia were radially elongated in contrast to the short type found in Lycopodium and Selaginella. In the megasporangia the number of spores was greater than in Selaginella. The spores resemble those of living heterosporous genera, though some were apparently very large and with prominent and complex ornamentation.

From the Devonian up to the present day we have evidence of the existence of land plants with jointed stems, and leaves borne in whorls at the nodes. In some the sporangia are borne on sporophylls, while in others they are borne on stalked sporangiophores. These plants, united in the phylum ARTICULATALES, include the orders:

I. PROTOARTICULATINEAE.

Plants with bifurcate leaves and pendulous naked sporangia.

II. Sphenophyllineae.

Herbaceous creeping plants, with slender articulate stems bearing whorls of wedge-shaped leaves. The strobili are built up of a series of whorls of leaf-like bracts, fused together for about half their length so that each whorl forms a cup round the axis of the strobilus. Attached to the axis immediately above the bracts is a whorl of slender pedicels, each terminating in a sporangium. The spores are all of one kind, about 90 μ in diameter, and bear spines connected by ridges on their surfaces (Knox, 1938, fig. 120).

III. Equisetineae.

Included with Equisetum are a large number of extinct forms with striking resemblances to the living genus. Commonest amongst the fossils of this order are the members of the family *Calamitaceae*. The characteristic sporangium-bearing organ is the sporangiophore. The spores were produced in tetrads, and fully formed spores are smooth and usually all about the same size, though in some species (e.g. *C. casheana*) small abortive spores are found with larger ones in the same sporangium (Hirmer, 1927).

The third division of vascular plants which differentiated from the psilophytalean complex was the Filicales, characterised by large leaves and, as a rule, with sporangia borne upon abaxial surfaces. The spores of these plants are somewhat diverse and are found in considerable numbers in coal-seams. The Filicales are, however, outwith the scope of the present survey, and the classification of the group need not be detailed here.

Members of these several phyla, Lycopodiales, Articulatales and Filicales, were among the dominant plants of the Palaeozoic swamps; it is the remains of this vegetation which has gone in large measure to the formation of coal.

In recent years the application of the study of palaeobotany has become of increasing value in correlation of coal-seams, particularly in relation to the search for coal and oil. The plant remains, including microfossils, of a given stratum may help not only to determine its age and mode of deposition, but also the climate and physiographic environment under which the plants lived.

Coal may be studied from many angles, physical, chemical or biological; the biological alone is dealt with here. One of the most recent developments in the microscopic study of coal has been the correlation of seams by means of spores and other microfossils.

"Because of their unique adaptation for dispersal and their numerical abundance in many sedimentary deposits, it is expected that spores will become of greater practical significance than many of the larger types of plantfossils that are more commonly noted by the geologist" (Schopf, 1944). Continental workers for some time have used megaspores for this purpose with considerable success (Zerndt, 1934, 1937; Dijkstra, 1946, 1949). In Great Britain microspore analysis has been more frequently employed; it is with the microspores that we are concerned at present. Various kinds of coal, particularly cannels and dull coals, contain vast numbers of spores, of which the cutinised spore coat is usually very resistant and well preserved. It is generally possible to remove these spores from the surrounding mineral and plant matrix and isolate them for precise study. It is seldom possible, however, to determine the parent plant from which the spores or detached fragments came, though various methods have been devised for determining the parentage of some types of spores. Hartung (1933) has published a careful study of the spores from macerated calamarian cones which can be compared with spores isolated from coals. The peel method has also been used successfully for fern sporangia (Radforth, 1938).

The typical accumulations of coal with which the geologists in this country are most familiar are chiefly of Carboniferous age. Carbonaceous sediments composed to a large extent of plant material are found also in other parts of the world in Devonian sediments; the earliest recorded occurrence of spores with the tetrad scar is from a kerosene shale from Sweden, of Upper Cambrian age, but their botanical affinity is unknown.

The immense number and variety of microspores found in coals is an indication of the richness of the vegetation in Palaeozoic times. The flora of the Carboniferous period was particularly luxuriant; and a definite sequence and evolution of plant types can be traced with a gradual shift in the dominance of various groups. In the Lower Carboniferous the chief components of the vegetation belong to the *Sphenophyllales*, *Lepidodendrales* and *Coenopterid* ferns; while later, the *Cordaitales* begin to diversify and become conspicuous. The Upper Carboniferous is marked by a great development of ferns and pteridosperms, and the extinction of the older forms of Lepidodendron, Sigillaria, Calamites and Neuropteris.

It might therefore be expected that in the Lower Carboniferous the greatest number of spores with definite Lycopodalean affinity would occur, with a small admixture of spores of filicinean origin; this is recognised to be the case.

In Great Britain most of the work on spore analysis of coal has been confined to the Middle Coal Measures, and, save for a short paper on the microspores of the Limestone Coal Group in Scotland by the present author (1948), little account has been taken of the spores of the Lower Carboniferous strata; thus a representation of the relative proportions of spore types during different periods can only be roughly estimated at present for this country.

An interesting summary has been given, however, by Naumova (1937) for coals of the U.S.S.R. Her conclusions are in agreement with the facts so far recorded of the spore content of the coals of the Carboniferous in Scotland. Naumova records a total of 400 forms of spores and pollen from the coal basins and deposits of the U.S.S.R. of different ages from the Devonian to the Tertiary. The number described from the Palaeozoic is 190, from the Mesozoic 154 and from the Cenozoic 65. In the Palaeozoic era spores with a triradiate slit, which Naumova terms Triletes Rimales, are predominant being developed up to 89 per cent., with 5 per cent. Monoletes and 2 per cent. Aletes; pollen appears towards the close of the era to the extent of 4 per cent. In the Mesozoic, although spores of the Triletes Rimales group continue to predominate, accounting for 60 per cent., an increasingly greater part is played by pollen of the Aporosa class (*i.e.* pollen without pores). An interesting point with regard to size is also mentioned—the forms with largest diameter, averaging 50–70 μ, are developed principally in the Palaeozoic strata, whereas in the Mesozoic the average diameter is 40–50 μ. In the Devonian of the U.S.S.R., Naumova states that the complex of spores consists solely of forms of the Triletes group, and the exine usually has sculpturing in the form of tubercles, spines or hooks; many of the types are similar to those found in the Lower Carboniferous. Here again only Trilete spores are encountered, among which forms with thickened margin, probably Lepidodendroid, constitute about 75 per cent. The Upper Carboniferous complex consists mostly of forms of the Triletes group but with a small proportion of Monoletes; the latter with sculpturing of a coniferous type. Among the Triletes, spores with reticulate ornamentation appear, and those with a thickened border become rare. The Permian assemblage is similar to that of the Upper Carboniferous; the main distinction being in less diversity of form and the appearance of coniferous pollen with two air-sacs.

It is significant that in the Devonian and Lower Carboniferous only spores of the Trilete group have been recorded from the U.S.S.R. —a fact which pertains also in Scotland, and which tends to strengthen the supposition that the vegetation at that time consisted mainly of *Lepidodendrales*, *Equisetales* and *Sphenophyllales*. The ferns, in which some genera have monolete spores, and gymnospermic plants apparently did not gain ascendancy until Upper Carboniferous times. In Scotland the microspore content of the Productive Coal Measures (Knox, 1942, 1946) is similar to that recorded for the coals of the Middle Coal Measures in England (Raistrick, 1933, 1934; Millott, 1939), and the spore types recorded from both resemble in general the types from corresponding measures in the U.S.S.R.

Since it is not possible to determine the parent plant from which the spores have come, in the early work on microfossils of coal in this country, spores were classified according to an artificial system, different *groups* being referred to by letters, and different *types* by numbers, A1, B1, etc. In the Coal Measures of the Upper Carboniferous of Great Britain the monolete, bilateral, smooth spore, designated B1, becomes a common constituent. This is a type which recurs amongst living ferns in widely separated genera, and the frequency of its occurrence in Upper Carboniferous strata is probably due to prevalence at that time of ferns in the vegetation of the coal swamps. This spore, B1, is not the same as that mentioned by Naumova as occurring in the Upper Carboniferous of the U.S.S.R.; she stresses monolete spores with exospore of the coniferous type. Similar gymnospermic forms are recorded from Britain, but they are not common.

The spores of only a small number of fossil plants are known with certainty; of these, the microspores of *Lepidostrobus Jacksoni* and *Lepidostrobus Oldhamius* (Kidston, 1923) are amongst the most easily recognised, and they are indistinguishable from the type D1 of Raistrick (1933). Other known spores, of a smooth round type, are those of plants belonging to the *Calamitaceae* (Hartung, 1933, Walton, 1948); those of *Mazocarpon oedipternum* (Schopf, 1941) with a papillate exospore; the granular spores of *Crosstheca Hughesiana* and *Crosstheca Hoeninghausi* (Kidston, 1923); the small triangular spores of the pteridosperm *Renaultia gracilis* and the large spherical spinose variety *Sphenophyllum Dawsoni* (Knox, 1938, figs. 118 and 120).

Classification of Fossil Spores.

A natural classification of fossil spores is at present practically impossible, since few of the spores so far described have been found in organic connection with the parent plant. It is thus necessary to formulate an artificial system using the various morphological features which have been found to be of diagnostic value.

Several systems have been proposed from time to time by different authors; these schemes are fundamentally the same, and employ as their primary division the form of dehiscence slit, *i.e.* whether tri-radiate or longitudinal. Wodehouse (1935, p. 135) is of the opinion that the "form and character of the germinal furrows are generally strictly phyletic, tending to be constant throughout families and other groups".

Schopf (1944) says that "The classification of spores admittedly presents many difficulties. When attempt is made to classify spores in accordance with the standard taxonomy, apparently inconsistent situations arise. In part this is because taxonomy of higher plants is almost entirely based on structures of the sporophyte, whereas spores belong to the gametophyte generation. The fact that Palaeozoic plant genera are extinct further complicates the problem, so that their treatment must necessarily be different from that used by students of Cenozoic and Recent spores or pollen". Moreover, it would appear that from time to time in quite diverse families of the plant kingdom, differences in spores and pollen attained maximum development, irrespective of the stage in the evolutionary process reached by the family. The Pteridophytes are frequently strongly differentiated in many parts of the plant body, and during Palaeozoic times, when they represented the most important forms of plant life, many diverse types are recognised which had adapted themselves to several ecological situations which are now largely occupied by so-called higher plants. It is a striking fact that the spores of these Palaeozoic plants were already highly organised and varied.

The classification of Potonie (1931) was one of the first to be used for stratigraphical purposes. He gave the generic name *Sporonites* to all spores, and added a descriptive prefix to designate a genus, as for example *Laevigato-sporonites*. According to Potonie, the earlier method of dividing the trilete spores into *Laevigato-*, *Apiculati-* and *Zonales* required revision.

Raistrick (1934), in England, employed the same distinguishing characters, but formulated a simpler nomenclature, using a letter and number as A1, B3, etc.; the letter being indicative of a generic form and the number of a specific character. In all he recognised 7 genera, A to G, and some 70 species.

The Russian scheme of Naumova (1937) approaches more closely to the German, giving prominence to the form of dehiscence slit and to the nature of the sculpturing.

The most recent and comprehensive system is that of the American authors Schopf, Wilson and Bentall (1944). It incorporates, as far as possible, all previously published work, and in their "Annotated Synopsis of Palaeozoic Fossil Spores" (1944) the guiding principles on which they base their classification are stated. It is pointed out by them that "the species classified under the same generic name must possess significant characteristics in common", and that "the essential validity of any classification depends on the relative significance that attaches to the various bio-characters". In the system promulgated by these three authors, 15 genera for microspores are recognised. The genera are distinguished by differences in symmetry, sculpturing and, to some extent, size, and each spore is given a generic and specific name, e.g. *Punctati-sporites punctatus*. The system has the advantage that it can easily be extended, the number of species added to, or the number of genera increased, as occasion demands.

In Great Britain, the classification of Raistrick, useful as it was in the early stages of spore analysis, is now found to be inadequate; it has been felt for some time that a binomial nomenclature should be adopted, thus enabling comparison to be made of work in this country, America and Europe. A universally recognised system has also the advantage that correlation on a wider scale can be effected, and problems of plant distribution and migration during Palaeozoic times can be viewed more satisfactorily.[1]

The study of the microspores of living representatives of the Lycopodiales, and their arrangement into groups having spores with closely similar ornamentation, can now serve as a basis for the classification of fossil spores. The application of this principle to fossil spores will give an indication of the advisable limits which should be set for any group or "form" genus as regards size and variety of ornamentation. It has been proved elsewhere (Knox, 1949) that in archegoniate plants, even during development, the nature of the ornamentation, or the variety of the processes with which the spores will ultimately be adorned, remains constant. A pointed, conical excrescence does not change during growth to a tuberculate or rod-like elevation; thus in any arbitrary classification it is safe to place all the spores with spinose ornamentation in the same group, since by so doing even a juvenile spore with spines will be included with the fully developed adult. Recognition of this fact will necessitate a wider range of size in a genus, so as to include the immature with the mature spores of the same species. In order to segregate those spores possessing the same type of process and external morphology, some of the larger "genera" proposed by Schopf, Wilson and Bentall (1944) will require to be subdivided and altered. This applies particularly to the genera *Punctati-sporites* and *Granulati-sporites*, which include spores with several different types of ornamentation. As regards the division into monolete and trilete, the former, which are oval and bean-shaped spores, have been kept in a genus by themselves, following Schopf, Wilson and Bentall, so long as the longitudinal slit is clearly visible and the exospore is smooth, granular or finely punctate.

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[1] Since the present paper was written, an account of "Research in Coal Palaeobotany since 1943" by J. M. Schopf (Econ. Geol., xliv, No. 6, 1949) has been received. It contains a full and comprehensive survey of the present position of microspore classification, and also a review of recent "spore" literature.

In the following pages these emendations, rearrangements and subdivisions are set out as suggestions. Four new genera have been proposed to accommodate the spores which do not easily fit into the existing scheme. These genera have been named *Spinoso-sporites*, *Plani-sporites*, *Verrucoso-sporites* and *Microreticulati-sporites*; they include spores with spinose, smooth, tuberculate and reticulate exospores respectively. Besides the spores referred to the new genera, three others have been transferred to different genera; they are *Punctati-sporites auriculaferens* placed in *Triquitrites* (fig. 273), *Cirratriradites zonalis* placed in *Endosporites* (fig. 295), and *Raistrickia abditus* placed in *Verrucoso-sporites*. The generic names used by Schopf, Wilson and Bentall have been maintained when their definition has not been altered. The individual spores are listed with the specific name recognised by these authors, and also the spores assigned to the new genera. The descriptions and figures given by Ibrahim (1932, 1933), Loose (1932, 1934) and others have been copied from the original publications, although in some cases these descriptions and figures are inadequate. Additional types from Great Britain are appended in their appropriate group, and references to the original publication given with each type.

Key to Genera of Palaeozoic Microspores.

(Adapted from the key of L. R. Wilson in Pollen Analysis Circular, No. 8.)

A. Spores with bilateral symmetry; monolete suture.
  B. Vesicular appendages lacking . . . . . VII. *Laevigato-sporites*
BB. Vesicular appendages one or two.

C. Two vesicular appendages attached opposite on central body	XII. *Alisporites*
CC. One vesicular appendage, annulate	XVII. *Florinites*
AA. Spores with tri-radial symmetry; trilete sutures.	
B. Vesicular appendages present.	
C. Vesicular appendage single	XIII. *Endosporites*
CC. Vesicular appendages trimerous	VI. *Alati-sporites*
BB. Vesicular appendages not present.	
C. Spores spherical; wall thin; ornamentation absent or very slight	XIV. *Calamospora*
CC. Spores spherical or triangular; ornamentation conspicuous.	
D. Equatorial region fimbriate, flanged, thickened or auriculate.	
E. Auriculate thickenings at radial angles	IX. *Triquitrites*
EE. No auriculate thickenings at angles.	
F. Fimbriate flanges longer between radii than at angles	XV. *Reinschospora*
FF. Flange not as above.	
G. Equatorial region thickened	VIII. *Denso-sporites*
GG. Equatorial region not thickened.	
H. Flange broad and membranous	XI. *Cirratriradites*
HH. Flange narrow, uniform width	X. *Lycospora*
DD. Equatorial region without flange or thickening.	
E. Wall thickening reticulate.	
F. Alveoli less than 6 μ across	IV. *Microreticulati-sporites*
FF. Alveoli more than 6 μ across	V. *Reticulati-sporites*
EE. Wall thickening not reticulate.	
F. Ornamentation absent or granular. Spore margin entire or nearly so	II. *Plani-sporites*
FF. Ornamentation of variously shaped processes clearly visible on margin.	
G. Ornamentation of sharp, pointed processes	I. *Spinoso-sporites*
GG. Ornamentation not as above.	
H. Ornamentation of blunt, straight-sided partate processes	XVI. *Raistrickia*
HH. Ornamentation of rounded, warty or tuberculate processes	III. *Verrucoso-sporites*

GENUS I. SPINOSO-SPORITES Knox, gen. nov.

Spores tetrahedral, trilete, triangular to spherical; 25–75 μ in diameter. Ornamentation of sharp, pointed, conical processes, variable in length, breadth and distance apart.

Key to the Species.

A. Spores triangular in shape.	
B. Spore diameter 50 μ or more; spines 5–7 μ long	*S. falcatus*, fig. 205
BB. Spore diameter less than 40 μ.	
C. Spines 2 μ long	*S. microsaetosus*, fig. 203
CC. Spines 3–4 μ long, 2 μ broad	*S. microspinosus*, fig. 204
AA. Spores spherical to ovoid in shape.	
B. Spore diameter 55–75 μ.	
C. Spinous processes minute, appearing granular	*S. latigranifer*, fig. 200

CC. Spinous processes very small . . .	*S. spinulistratus*, fig. 202
BB. Spore diameter less than 60 μ.	
C. Spore diameter 45–60 μ.	
D. Spinous processes 3 × 1 μ, widely spaced .	*S. aculeatus*, fig. 198.
DD. Spinous processes 1 μ long, closely spaced	*S. globosus*, fig. 199
CC. Spore diameter 25–45 μ.	
D. Spines long, 5–8 μ	*S. echinatus*, fig. 208
DD. Spines short, less than 2 μ.	
E. Processes ciliate	*S. ciliatus*, fig. 206
EE. Processes fine teeth.	
F. Teeth 1·5 μ	*S. spinosus*, fig. 201
FF. Teeth less than 1 μ	*S. denticulatus*, fig. 207

Spinoso-sporites aculeatus (Ibr.) Knox, comb. nov. Fig. 198.
Punctati-sporites aculeatus (Ibr.) S. W. & B.[1]

Spherical to ovate, 48–53 μ. Tri-radiate mark 2/3 radius. Wall 2 μ. Spines 3 μ in length, 1 μ broad at base; set 2–4 μ apart.

Probably equivalent to *E5* (Raistrick).

Spinoso-sporites ciliatus Knox, nom. nov. Fig. 206. *E1* of Raistrick.

Spherical, 35–50 μ. Tri-radiate mark 2/3 radius. Surface varying from finely punctate to granular, usually with fine, hair-like processes easily seen on periphery.

Spinoso-sporites denticulatus Knox, nom. nov. Fig. 207. *E2* of Raistrick.

Spherical, 30–45 μ. Tri-radiate mark faintly visible or absent. Surface punctate to finely toothed; teeth seen on the margin.

Spinoso-sporites echinatus Knox, nom. nov. Fig. 208.

Spherical, 25 μ. Tri-radiate mark 1/3 radius. Surface with acicles 5–8 μ long and spaced about 5 μ apart.

Spinoso-sporites falcatus Knox, nom. nov. Fig. 205. *18K* (Knox, 1948).

Triangular, 55 μ. Tri-radiate mark extending to the margin. Surface with spinose processes, 5–7 μ long, straight or curved and spaced 3–5 μ apart.

Spinoso-sporites globosus (Loose) Knox, comb. nov. Fig. 199.
Punctati-sporites globosus (Loose) S. W. & B.

Spherical to elliptical, 44–60 μ. Tri-radiate mark 2/3 radius. Spines small, 1 μ; margin with fine prickles.

Probably equivalent to *B6* (Raistrick).

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[1] For further synonymy see the paper by Schopf, Wilson and Bentall (1944).

Spinoso-sporites latigranifer (Loose) Knox, comb. nov. Fig. 200.
Punctati-sporites latigranifer (Loose) S. W. & B.

Ovoid, 55–78 μ. Ornamentation faintly spinose, spines 1 μ. Exospore with fine prickles appearing granular.

Spinoso-sporites microsaetosus (Loose) Knox, comb. nov. Fig. 203.
Granulati-sporites microsaetosus (Loose) S. W. & B.

Triangular, 26–39 μ. Tri-radiate mark 2/3 radius. Setose, bristles 2–2·5 μ; margin bristly to prickly.

Probably equivalent to *D8* (Raistrick).

Spinoso-sporites microspinosus (Ibr.) Knox, comb. nov. Fig. 204.
Granulati-sporites microspinosus (Ibr.) S. W. & B.

Triangular, 34–39 μ. Tri-radiate mark 2/3 radius. Spinose, spines 3–4 μ long and 2 μ broad at base.

Probably equivalent to *17K* (Knox, 1948).

Spinoso-sporites spinosus (Loose) Knox, comb. nov. Fig. 201.
Punctati-sporites spinosus (Loose) S. W. & B.

Spherical, 36–41 μ. Spiny to faintly verrucose; prickles 1·5 μ broad; margin shows broad, blunt prickles.

Spinoso-sporites spinulistratus (Loose) Knox, comb. nov. Fig. 202.
Punctati-sporites spinulistratus (Loose) S. W. & B.

Ovoid to round, 54–72 μ. Tri-radiate mark 2/3 radius. Surface covered with fine spines.

Probably equivalent to *B4* (Raistrick).

GENUS II. PLANI-SPORITES Knox, gen. nov.

Spores tetrahedral, trilete, spherical to rounded-triangular; 25–130 μ in diameter. Ornamentation absent or granular to punctate or finely papillate. Margin of spore entire or nearly so.

Key to the Species.

A. Spores oval to spherical in shape.	
B. Spore diameter less than 40 μ . . .	*P. parvipunctatus*, fig. 212
BB. Spore diameter greater than 40 μ.	
C. Spores oval, large, 80–150 μ; exospore finely granular	*P. ovatus*, fig. 222
CC. Spores almost spherical, 45–95 μ.	
D. Exospore minutely tuberculate .	*P. microtuberosus*, fig. 211
DD. Exospore granular.	
E. Margin smooth	*P. punctatus*, fig. 213
EE. Margin finely notched.	
F. Spore diameter 45–75 μ . .	*P. aureus*, fig. 209
FF. Spore diameter 70–95 μ . .	*P. granifer*, fig. 210

AA. Spores triangular in shape.
  B. Sides of spore concave.
    C. Exospore smooth . . . . *P. deltiformis*, fig. 215
    CC. Exospore not smooth.
      D. Exospore faintly granular.
        E. Spore diameter greater than 65 μ . *P. deltoides*, fig. 216
        EE. Spore diameter less than 40 μ . *P. piroformis*, fig. 219
      DD. Exospore papillate . . . *P. verrucosus*, fig. 221
  BB. Sides of spore straight or convex.
    C. Exospore smooth.
      D. Spore diameter 35 μ; wall thin . *P. priddyi*, fig. 220
      DD. Spore diameter greater than 40 μ.
        E. Wall 3 μ thick . . . . *P. crassus*, fig. 223
        EE. Wall 1·5 μ thick . . . . *P. sphaerotriangulatus*, fig. 214
    CC. Exospore granular.
      D. Margin rough . . . . *P. granulatus*, fig. 217
      DD. Margin smooth . . . . *P. micrograinfer*, fig. 218

Plani-sporites aureus (Loose) Knox, comb. nov. Fig. 209.
Punctati-sporites aureus (Loose) S. W. & B.

Oval to round, 45–75 μ. Tri-radiate mark 1/3 radius. Surface faintly reticulate to punctate; margin very finely notched.

Plani-sporites crassus Knox, nom. nov. Fig. 223. *11K* (Knox, 1948).

Triangular, 65–80 μ. Tri-radiate mark 2/3 radius, surrounded by a translucent area. Wall 3 μ thick; surface smooth.

Plani-sporites deltiformis (S. W. & B.) Knox, comb. nov. Fig. 215.
Granulati-sporites deltiformis S. W. & B.

Triangular, sides concave, 26–30 μ. Surface smooth, without ornamentation.

Plani-sporites deltoides (Ibr.) Knox, comb. nov. Fig. 216.
Granulati-sporites deltoides (Ibr.) S. W. & B.

Triangular, 65–77 μ. Tri-radiate mark extending to the margin. Surface smooth to faintly punctate. Margin smooth.

Plani-sporites granifer (Ibr.) Knox, comb. nov. Fig. 210.
Punctati-sporites granifer (Ibr.) S. W. & B.

Triangular to spherical, 70–95 μ. Tri-radiate mark 2/3 radius. Wall 2–3 μ; surface granular; at margin granules 3–4 μ apart.

Plani-sporites granulatus (Ibr.) Knox, comb. nov. Fig. 217.
Granulati-sporites granulatus Ibr.

Triangular, 25–34 μ. Tri-radiate mark 2/3 radius. Surface granulate; margin rough.

Plani-sporites micrograinfer (Ibr.) Knox, comb. nov. Fig. 218.
Granulati-sporites micrograinfer Ibr.

Triangular, 31–35 μ. Tri-radiate mark extending to the margin; surface granular.

Plani-sporites microtuberosus (Loose) Knox, comb. nov. Fig. 211.
Punctati-sporites microtuberosus (Loose) S. W. & B.

Ovoid to spherical, 58–84 μ. Tri-radiate mark 2/3 radius. Exospore covered with fine, small (1 μ) tubercles, closely set; margin finely granular.

Plani-sporites ovatus Knox, nom. nov. Fig. 222. *6K* (Knox, 1942).

Oval, 80–150 μ long. Tri-radiate mark 1/3 radius, frequently open. Surface very finely granular.

Plani-sporites parvipunctatus (Kosanke) Knox, comb. nov. Fig. 212.
Punctati-sporites parvipunctatus Kosanke

Almost spherical, 32–38 μ. Wall 2 μ. Tri-radiate mark faint, 2/3 radius. Exospore faintly punctate.

Plani-sporites piroformis (Loose) Knox, comb. nov. Fig. 219.
Granulati-sporites piroformis Loose

Triangular, 26–40 μ. Tri-radiate mark extending to the margin. Surface faintly granular.

Probably equivalent to *D4* (Raistrick).

Plani-sporites priddyi (Berry) Knox, comb. nov. Fig. 220.
Granulati-sporites priddyi (Berry) S. W. & B.

Triangular, 35 μ. Tri-radiate mark 2/3 radius. Wall thin, often slightly convex; surface smooth.

Plani-sporites punctatus (Ibr.) Knox, comb. nov. Fig. 213.
Punctati-sporites punctatus Ibr.

Round to triangular, 50–77 μ. Tri-radiate mark extending to the margin. Surface punctate; margin smooth or slightly rough.

Probably equivalent to *B5* (Raistrick).

Plani-sporites sphaerotriangulatus (Loose) Knox, comb. nov. Fig. 214.
Punctati-sporites sphaerotriangulatus (Loose) S. W. & B.

Triangular, 40–57 μ. Tri-radiate mark 2/3 radius. Surface smooth to faintly punctate; margin smooth; wall 1·5 μ thick.

Plani-sporites verrucosus (Wilson & Coe) Knox, comb. nov. Fig. 221.
Granulati-sporites verrucosus (Wilson & Coe) S. W. & B.

Tri-radial, sides concave, 23–26 μ. Exine papillate.

Genus III. Verrucoso-sporites Knox, gen. nov.

Spores tetrahedral, trilete; spherical to triangular; 25–120 μ in diameter. Ornamentation of rounded, warty or tuberculate processes; visible as rounded elevations at the margin.

Key to the Species.

A. Spores spherical to ovoid in shape.	
B. Spores large, over 100 μ.	
C. Exospore coarsely tuberculate; tubercles 6–8 × 3–4 μ, widely spaced	*V. tuberosus*, fig. 236
CC. Exospore papillate; papillae 5 μ apart	*V. maculosus*, fig. 237
BB. Spore diameter less than 90 μ.	
C. Tubercles 2–4 μ, closely spaced.	
D. Spores oval, 54 × 39 μ; margin smooth	*V. tuberculatus*, fig. 231
DD. Spores spherical.	
E. Spore diameter 70–80 μ	*V. morulatus*, fig. 235
EE. Spore diameter 70–108 μ	*V. verrucosus*, fig. 230
	V. grandiverrucosus
CC. Tubercles 3–10 μ long.	
D. Spores oval, tubercles 6–10 μ	*V. abditus*
DD. Spores oval to spherical; tubercles 3–7 μ.	
E. Tubercles 3–5 μ; margin smooth	*V. bucculentus*, fig. 224
EE. Tubercles 3–7 μ; margin wavy	*V. microverrucosus*, fig. 228
AA. Spores triangular to spherical.	
B. Tuberculate processes broad and low.	
C. Tubercles irregular, up to 7 μ, broad	*V. grumosus*, fig. 226
CC. Tubercles large, 7–12 μ, broad and flat	*V. papillosus*, fig. 229
BB. Tuberculate processes 2–4 μ.	
C. Processes 3–4 μ long.	
D. Spore diameter 38–55 μ	*V. triquetris*, fig. 233
DD. Spore diameter 57–62 μ	*V. firmus*, fig. 225
CC. Processes 2–3 μ.	
D. Spore diameter less than 50 μ	*V. gibbosus*, fig. 232
DD. Spore diameter greater than 50 μ	*V. insignitis*, fig. 227

Verrucoso-sporites abditus (Loose) Knox, comb. nov.
Raistrickia abditus (Loose) S. W. & B.

Oval, 65–78 μ. Exospore 5 μ. Tri-radiate mark very faint. Surface tuberculate; tubercles 6–10 μ long.

Verrucoso-sporites bucculentus (Loose) Knox, comb. nov. Fig. 224.
Punctati-sporites bucculentus (Loose) S. W. & B.

Ovoid, 38–55 μ. Tri-radiate mark extending to the margin. Surface verrucose; tubercles 3–5 μ; margin with small tubercles visible.

Probably equivalent to *E4* (Raistrick).

Verrucoso-sporites firmus (Loose) Knox, comb. nov. Fig. 225.
Punctati-sporites firmus (Loose) S. W. & B.

Round to triangular, 57–62. Tri-radiate mark 2/3 radius. Surface verrucose, tubercles 3–6 μ; on the margin, elevations appear 3–4 μ long.

Probably equivalent to *D3* (Raistrick).

Verrucoso-sporites gibbosus (Ibr.) Knox, comb. nov. Fig. 232.
Granulati-sporites gibbosus (Ibr.) S. W. & B.

Triangular, 42–46 μ. Tri-radiate mark 2/3 radius. Surface tuberculate; tubercles 2–3 μ broad and 2–3 μ long.

Verrucoso-sporites grandiverrucosus (Kosanke) Knox, comb. nov.
Punctati-sporites grandiverrucosus Kosanke

Spherical, 73–92 μ. Wall 1–3 μ. Ornamentation characteristically verrucose; margin irregular.

Verrucoso-sporites grumosus (Ibr.) Knox, comb. nov. Fig. 226.
Punctati-sporites grumosus (Ibr.) S. W. & B.

Triangular to spherical, 54–85 μ. Tri-radiate mark 2/3 radius. Surface verrucose.

Verrucoso-sporites insignitis (Ibr.) Knox, comb. nov. Fig. 227.
Punctati-sporites insignitis (Ibr.) S. W. & B.

Round to triangular, 50–78 μ. Surface bearing granules, sometimes small spines, 3–4 μ long. At the margin these processes appear as warty protuberances.

Verrucoso-sporites maculosus Knox, nom. nov. Fig. 237. *23K* (Knox, 1948).

Spherical, 100–120 μ. Tri-radiate mark 2/3 radius. Surface ornamented with small papillae, visible as slight elevations at the margin, regularly arranged 5 μ apart; between the papillae the surface is finely granular.

Verrucoso-sporites microverrucosus (Ibr.) Knox, comb. nov. Fig. 228.
Punctati-sporites microverrucosus (Ibr.) S. W. & B.

Ovate to spherical, 38–74 μ. Tri-radiate mark extending to the margin. Surface tuberculate; tubercles 3–7 μ long. Margin faintly wavy.

Verrucoso-sporites morulatus Knox, nom. nov. Fig. 235. *20K* (Knox, 1948).

Spherical, 70–80 μ. Tri-radiate mark 1/3 radius. Surface closely covered with short tuberculate processes, 2–3 μ long.

Verrucoso-sporites papillosus (Ibr.) Knox, comb. nov. Fig. 229.
Punctati-sporites papillosus (Ibr.) S. W. & B.

Triangular to round, 74–98 μ. Tri-radiate mark 2/3 radius. Surface tuberculate; tubercles 7–12 μ long and 4–8 μ broad; warts mainly flattened and of various shapes.

Verrucoso-sporites triquetris (Ibr.) Knox, comb. nov. Fig. 233.
Granulati-sporites triquetris (Ibr.) S. W. & B.

Triangular, 38–58 μ. Tri-radiate mark extending to the margin. Surface tuberculate; tubercles round to flattened, 3–4 μ long.

Verrucoso-sporites tuberculatus (Berry) Knox, comb. nov. Fig. 231.
Laevigato-sporites tuberculatus (Berry) S. W. & B.

Oval, 54 × 39 μ. Wall thin. Surface tuberculate; tubercles not visible at the edge of the spore.

Verrucoso-sporites tuberosus Knox, nom. nov. Fig. 236. *21K* (Knox, 1948).

Spherical to ovate, about 100 μ in diameter. Tri-radiate mark 1/3 radius. Surface ornamented with rounded processes 6–8 μ long, 3–4 μ broad and spaced 5–7 μ apart.

Verrucoso-sporites verrucosus (Ibr.) Knox, comb. nov. Fig. 230.
Punctati-sporites verrucosus (Ibr.) S. W. & B.

Ovoid to round, 65–108 μ. Tri-radiate mark 2/3 radius. Surface warty; warts 2–4 μ.

GENUS IV. MICRORETICULATI-SPORITES Knox, gen. nov.

Spores tetrahedral, trilete or bilateral, monolete; spherical to triangular or oval; 14–70 μ in diameter. Ornamentation reticulate with fine, small mesh not more than 6 μ across, or with interrupted ridges, irregular in shape and disposition.

Key to the Species.

A. Spores spherical, ovoid or polygonal in shape.	
B. Exospore with interrupted ridges.	
C. Spores bilateral	*M. Thiessenii*, fig. 250
CC. Spores tetrahedral.	
D. Spores spherical	*M. corrugatus*, fig. 238
DD. Spores ovoid	*M. velatus*, fig. 245
BB. Exospore reticulate.	
C. Spinose processes projecting from the margin.	
D. Spore diameter 45 μ, processes 5–7 μ long	*M. spicatus*
DD. Spore diameter 25–30 μ, processes 3 μ long	*M. spinulosus*
CC. Margin irregular, without spinose processes.	
D. Spore diameter greater than 35 μ.	
E. Mesh 2–4 μ	*M. lunatus*
EE. Mesh 4–6 μ.	
F. Bars extending over margin . .	*M. reticulocingulum*, fig. 243
FF. Margin wavy	*M. cusus*, fig. 239 *M. faveolatus* *M. maculatus*, fig. 241
DD. Spore diameter less than 35 μ.	
E. Mesh 2–3 μ	*M. microreticulatus*
EE. Mesh 1–2 μ.	
F. Spore diameter 15 μ . . .	*M. minutus*
FF. Spore diameter 35 μ . . .	*M. punctatus*
AA. Spores triangular in shape.	
B. Exospore rugose; margin notched . .	*M. torquifer*, fig. 248
BB. Exospore reticulate.	
C. Mesh 1–6 μ; bars thick.	
D. Mesh 1–3 μ; margin notched . .	*M. nobilis*, fig. 242
DD. Mesh 4–6 μ; margin wavy . .	*M. trigonus*, fig. 249
CC. Reticulation faint; bars delicate.	
D. Mesh 2–3 μ; margin almost smooth .	*M. lacunosus*, fig. 240
DD. Mesh 1–2 μ.	

E. Mesh 2 μ; margin toothed . . . *M. fistulosus*, fig. 246
EE. Mesh 1 μ.
F. Margin rough; spore diameter 23–32 μ . . . . . *M. parvus*, fig. 247
FF. Margin smooth; spore diameter 49–54 μ . . . . . *M. trigonoreticulatus*, fig. 244

Microreticulati-sporites corrugatus (Ibr.) Knox, comb. nov. Fig. 238.
Punctati-sporites corrugatus Ibr.

Spherical, 42–46 μ. Tri-radiate mark 2/3 radius. Surface reticulate to wrinkled; reticulum more or less broken up into separate irregular ridges.

Microreticulati-sporites cusus (Loose) Knox, comb. nov. Fig. 239.
Punctati-sporites cusus Loose

Ovoid to round, 47–57 μ. Tri-radiate mark extending to the margin. Surface reticulate; reticulum of sunken mesh 4–6 μ; outline slightly wavy; wall 2–3 μ.

Probably equivalent to *D6* (Raistrick).

Microreticulati-sporites faveolatus Knox, nom. nov. *26K* (Knox, 1948, fig. 32).

Spherical, 45–50 μ. Tri-radiate mark 1/3 radius. Surface reticulate; mesh regular, 4–6 μ; bars 1–2 μ thick and sometimes interrupted; margin sinous.

Microreticulati-sporites fistulosus (Ibr.) Knox, comb. nov. Fig. 246.
Granulati-sporites fistulosus (Ibr.) S. W. & B.

Triangular, 38–46 μ. Tri-radiate mark extending to the margin. Surface finely reticulate; mesh 2 μ; margin toothed.

Microreticulati-sporites lacunosus (Ibr.) Knox, comb. nov. Fig. 240.
Punctati-sporites lacunosus (Ibr.) S. W. & B.

Triangular, 49 μ. Tri-radiate mark 2/3 radius. Surface faintly microreticulate; reticulum 2–3 μ across.

Microreticulati-sporites lunatus Knox, nom. nov. *35K* (Knox, 1948, fig. 41).

Spherical, 45 μ. Tri-radiate mark extending to the margin. Exospore finely reticulate; mesh regular, 2–4 μ, bars 1–2 μ thick. Margin sinuous.

Microreticulati-sporites maculatus (Ibr.) Knox, comb. nov. Fig. 241.
Punctati-sporites maculatus (Ibr.) S. W. & B.

Polygonal to circular, 46–69 μ. Tri-radiate mark 2/3 radius. Surface reticulate; mesh 5–6 μ; margin coarsely toothed.

Probably equivalent to *F3* (Raistrick) and *25K* (Knox, 1948, fig. 31).

Microreticulati-sporites microreticulatus Knox, nom. nov. *36K* (Knox, 1948, fig. 42).

Spherical 30–35 μ, Tri-radiate mark 2/3 radius. Exospore finely reticulate. Mesh 2–3 μ; bars thin; margin of spore irregular.

Microreticulati-sporites minutus Knox, nom. nov. *32K* (Knox, 1948, fig. 38).

Spherical, 15 μ. Tri-radiate mark indistinct. Exospore microreticulate; mesh 1–2 μ; margin irregular.

Microreticulati-sporites nobilis (Wicher) Knox, comb. nov. Fig. 242.
Punctati-sporites nobilis (Wicher) S. W. & B.

Triangular, 30–40 μ. Tri-radiate mark 2/3 radius. Surface reticulate; mesh 1–3 μ; an irregular network covers the spore body; the bars of the mesh are relatively thick and rounded above; margin notched.

Possibly the same as *13K* (Knox, 1948, fig. 10).

Microreticulati-sporites parvus (Ibr.) Knox, comb. nov. Fig. 247.
Granulati-sporites parvus (Ibr.) S. W. & B.

Triangular, 23–32 μ. Tri-radiate mark 2/3 radius. Surface reticulate; reticulum fine, 1 μ; margin faintly rough.

Microreticulati-sporites punctatus Knox, nom. nov. *37K* (Knox, 1948, fig. 43).

Spherical, 35 μ. Tri-radiate mark indistinct. Exospore microreticulate; mesh 1–2 μ; margin irregular.

Microreticulati-sporites reticulocingulum (Loose) Knox, comb. nov. Fig. 243.

Punctati-sporites reticulocingulum (Loose) S. W. & B.

Spherical to ovoid, 35–56 μ. Tri-radiate mark very faint. Surface reticulate; mesh 4–5 μ; bars up to 2 μ broad and extending over the margin.

Probably equivalent to *F1* (Raistrick).

Microreticulati-sporites spicatus Knox, nom. nov. *27K* (Knox, 1948, fig. 33).

Spherical, 45 μ. Tri-radiate mark indistinct. Surface reticulate; mesh 4–6 μ, bars thin, bearing straight spinose processes 5–7 μ long at the corners of the mesh; these are seen at the periphery.

Microreticulati-sporites spinulosus Knox, nom. nov. *31K* (Knox, 1948, fig. 37).

Spherical, 25–30 μ. Tri-radiate mark indistinct. Exospore reticulate; mesh 3–4 μ; bars thin, seen projecting from the margin up to 3 μ.

Microreticulati-sporites Thiessenii (Kosanke) Knox, comb. nov. Fig. 250.
Laevigato-sporites Thiessenii Kosanke

Bilateral, monolete; oval, elongate; 14–24 μ; wall 1–2 μ. Surface loosely to sharply verrucose, forming intermittent ridges and valleys.

Microreticulati-sporites torquifer (Loose) Knox, comb. nov. Fig. 248.
Granulati-sporites torquifer (Loose) S. W. & B.

Triangular to polygonal, 29–42 μ. Tri-radiate mark 2/3 radius. Surface rugose and irregularly ridged; margin finely notched.

Microreticulati-sporites trigonoreticulatus (Loose) Knox, comb. nov. Fig. 244.
Punctati-sporites trigonoreticulatus (Loose) S. W. & B.

Triangular, 49–54 μ. Tri-radiate mark extending to the margin. Surface reticulate; mesh 1 μ.

Microreticulati-sporites trigonus (Ibr.) Knox, comb. nov. Fig. 249.
Granulati-sporites trigonus (Ibr.) S. W. & B.

Triangular, 27–46 μ. Tri-radiate mark 2/3 radius. Surface reticulate; mesh 4–6 μ across; margin wavy.

Microreticulati-sporites velatus (Loose) Knox, comb. nov. Fig. 245.
Punctati-sporites velatus (Loose) S. W. & B.

Elliptical, 41–57 μ. Surface reticulate to rugose.

GENUS V. RETICULATI-SPORITES (Ibrahim, 1933) emend., S. W. & B.

Spores radially symmetrical; spherical or moderately oblate; size ranges from 40 to 100 μ in diameter. Ornamentation coarsely and often irregularly reticulate.

Key to the Species.

A. Spore mesh less than 15 μ; lamellae 2–3 μ thick.	
B. Mesh 5–8 μ; spore diameter less than 55 μ .	*R. facetus*, fig. 252
BB. Mesh 7–14 μ.	
C. Spore diameter greater than 50 μ . .	*R. mediareticulatus*, fig. 253
CC. Spore diameter less than 50 μ.	
D. Spore diameter 40 μ	*R. favus*
DD. Spore diameter 25–30 μ . . .	*R. alveolatus*

AA. Spore mesh large; greater than 15 μ; lamellae thick.	
B. Spore diameter less than 65 μ; margin of lamellae frilled	*R. corporeus*, fig. 251
BB. Spore diameter greater than 65 μ.	
C. Spore margin with a membranous border.	
D. Mesh 13–23 μ; lamellae 3–5 μ	*R. reticuliformis*, fig. 256 *R. reticulatus*
DD. Mesh more than 25 μ; alveoli deep, with membranous flanges	*R. fimbriatus*, fig. 257
CC. Spore margin without a membranous border.	
D. Spore ovoid; lamellae 4–7 μ, warty	*R. ornatus*, fig. 254
DD. Spore polygonal; lamellae 6–8 μ, radiating from a central polygon	*R. polygonalis*, fig. 255

Reticulati-sporites alveolatus Knox, nom. nov. *34K* (Knox, 1948, fig. 40).

Spherical, 25–30 μ. Tri-radiate mark indistinct. Exospore reticulate; mesh 7–10 μ; alveoli deep, and lamellae with a thin membranous margin about 5 μ.

Reticulati-sporites corporeus Loose. Fig. 251.

Oval to polygonal, 60–65 μ. Tri-radiate mark 2/3 radius. Surface reticulate; mesh 18–23 μ across; the margins of the mesh structure appear frilled; they extend over the spore margin.

Reticulati-sporites facetus (Ibr.) S. W. & B. Fig. 252.

Circular, 42–55 μ. Surface reticulate; mesh 7–14 μ, bars 2 μ thick; margin smooth.

Probably equivalent to *F2* (Raistrick).

Reticulati-sporites favus Knox, nom. nov. *28K* (Knox, 1948, fig. 34).

Spherical, 40 μ. Tri-radiate mark extending to the margin. Exospore reticulate; mesh 10 μ, bars thin, and projecting at the margin 3 μ.

Reticulati-sporites fimbriatus Knox, nom. nov. Fig. 257. *5K* (Knox, 1942).

Spherical, 80–100 μ. Spore ornamented with prominent ridges forming deep hexagonal alveoli; the large-meshed network has membranous flanges which appear at the margin of the spore as a transparent wing.

Reticulati-sporites mediareticulatus Ibr. Fig. 253.

Polygonal to ovate, 58–65 μ. Tri-radiate mark 2/3 radius. Surface reticulate; mesh 7–14 μ, bars 2 μ thick; margin smooth.

Probably equivalent to *F2* (Raistrick).

Reticulati-sporites ornatus (Ibr.) S. W. & B. Fig. 254.

Oblate to polygonal, 70–108 μ. Tri-radiate mark 2/3 radius. Surface reticulate; mesh 15–23 μ, with warty bars 4–7 μ thick.

Reticulati-sporites polygonalis (Ibr.) S. W. & B. Fig. 255.

Polygonal to round, 88–108 μ. Tri-radiate mark 2/3 radius. Darker ring inside periphery; strong, large mesh with bars 6–8 μ thick, arranged with polygon over the centre and radial ribs from the angles to the periphery.

Probably equivalent to *C3* (Raistrick).

Reticulati-sporites reticulatus (Ibr.) S. W. & B.

Polygonal to round, 73–100 μ. Tri-radiate mark 2/3 radius. Surface reticulate; mesh 15–23 μ; ridges of mesh winding to frilly and 3–4 μ thick; mesh 4–5 μ, sided with smaller network connecting them 7–9 μ across. Round the spore is a lighter membrane 2–4 μ wide.

Reticulati-sporites reticuliformis Ibr. Fig. 256.

Polygonal to circular, 72–94 μ. Tri-radiate mark extending to the margin. Surface reticulate; mesh 13–17 μ; bars 3–5 μ thick; a thin membrane seen round the margin 5–7 μ broad.

GENUS VI. ALATI-SPORITES Ibrahim, 1933.

Spores radial, trilete; sub-triangular, with wings present. Ornamentation of the spore body may be punctate or finely reticulate. The spore coat consists of two distinct membranes; the outer membrane is thin, and expanded to form bladders in trimerous pattern.

Alati-sporites pustulatus Ibr. Fig. 258.

Triangular to round; spore body 49–55 μ in diameter. Tri-radiate mark extending to the margin. Surface of spore very finely reticulate; wings, 16–24 μ broad, punctate.

Probably equivalent to *D5* (Raistrick).

GENUS VII. LAEVIGATO-SPORITES (Ibrahim, 1933) emend., S. W. & B.

Spores bilateral, monolete; oval to bean-shaped. Spores range in size from 20 μ to over 130 μ in their long dimension. Ornamentation smooth to finely punctate.

Key to the Species.

A. Exospore smooth.
  B. Length of spore 60–75 μ . . . . . *L. desmoinensis*, fig. 260
  BB. Length of spore 21–29 μ . . . . . *L. minimus*, fig. 261

AA. Exospore not smooth.	
B. Exospore punctate.	
C. Length of spore 16–25 μ	*L. minutus*, fig. 262
CC. Length of spore 42–85 μ	*L. vulgaris*, fig. 264
BB. Exospore not punctate.	
C. Exospore reticulate	*L. bilateralis*, fig. 259
CC. Exospore papillate	*L. pennovalis*, fig. 263

Laevigato-sporites bilateralis (Loose) S. W. & B. Fig. 259.

Oval, monolete; 41–58 μ. Surface finely reticulate; periphery notched; wall 3–5 μ thick.

Laevigato-sporites desmoinensis (Wilson & Coe) S. W. & B. Fig. 260.

Bilateral, bean-shaped; monolete; 60–75 μ long and 39–42 μ wide. Wall transparent and unornamented.

Laevigato-sporites minimus (Wilson & Coe) S. W. & B. Fig. 261.

As *L. desmoinensis*; 21–29 μ long and 17–20 μ wide.

These two spore types are probably equivalent to *B1* (Raistrick).

Laevigato-sporites minutus (Ibr.) S. W. & B. Fig. 262.

Ovate, monolete; 16–25 μ. Surface punctate; margin rough.

Probably equivalent to *B8* (Raistrick).

Laevigato-sporites pennovalis Berry Fig. 263.

Ovate, 46 μ long and 31 μ broad; wall thicker at ends than sides. Surface sparingly covered with small papillae, evenly spaced but not visible at margin.

Laevigato-sporites vulgaris Ibr. Figs. 264 *a* and *b*.

Oval to bean-shaped; 42–85 μ. Surface smooth to faintly punctate.

GENUS VIII. DENSO-SPORITES (Berry, 1937) emend., S. W. & B.

Spores radially symmetrical, trilete; round to sub-triangular; size 35–100 μ in diameter. Ornamentation smooth to apiculate and rugose. The spore coat is characterised by great differences in thickness, being thin and membranous on the proximal and distal walls and thick in the equatorial region. Round the equator there may be a dense ring or a flange.

Key to the Species.

A. Equatorial ring smooth	*D. annulatus*, fig. 265 *D. covensis*
AA. Equatorial ring or flange bearing spines.	
B. Apical crest flanged	*D. pannosus*, fig. 267
BB. Apical crest smooth	*D. indignabundus*, fig. 266

Denso-sporites annulatus (Loose) S. W. & B. Fig. 265.

Oval to triangular, 25–45 μ. Tri-radiate mark extending to the margin. Spore surface smooth to finely punctate. Equatorial ring smooth; 5–10 μ thick.

Probably equivalent to *A1* (Raistrick).

Denso-sporites covensis Berry

Oval, 58 μ long and 50 μ broad. Wall very thick, about $\frac{1}{3}$ diameter, dark and opaque, smooth and even; central portion clear and trapezoidal in shape, margins clearly marked, no apparent connection between inside and outside.

Denso-sporites indignabundus (Loose) S. W. & B. Fig. 266.

Round, oval or polygonal; tri-radiate mark extending to the margin; 40–75 μ. Surface and margin with closely spaced spines about 1–2 μ long. In polar view a faint brownish equatorial rim runs concentrically and is up to 6 μ broad.

Probably equivalent to *A5* (Raistrick).

Denso-sporites pannosus Knox, nom. nov. Fig. 267. *9K* (Knox, 1948).

Sub-triangular, 50–75 μ. Tri-radiate mark extending to the margin. Surface of spore finely spinose; equatorial wing, fringed and irregularly and coarsely toothed; apical crest also with a fringed flange.

Genus IX. Triquitrites Wilson and Coe, 1940.

Spores trilete, radial; oval to elliptical in vertical plane; in equatorial plane triangular in outline with rounded or truncate corners; sides convex to strongly concave. Size 35–70 μ. Surface smooth to granular or verrucose.

Key to the Species.

A. Corner flanges truncate.	
B. Flanges 15–20 μ across.	
C. Exospore smooth	*T. arculatus*, fig. 268
CC. Exospore not smooth.	
D. Exospore granular	*T. tribullatus*, fig. 270
DD. Exospore warty	*T. papillosus*, fig. 234 *T. spinosus*, fig. 269
BB. Flanges 5–10 μ across	*T. auriculaferens*, fig. 273
AA. Corner flanges not truncate.	
B. Corners thickened and rounded . . .	*T. triturgidus*, fig. 272
BB. Spore bell-shaped	*T. trigonappendix*, fig. 271

Triquitrites arculatus Wilson and Coe Fig. 268.

Triangular, tri-radial, with concave sides and an equatorial flange conspicuously wider at the corners; 40–49 μ. Tri-radiate mark 2/3 radius. Surface without ornamentation.

Triquitrites auriculaferens (Loose) Knox, comb. nov. Fig. 273.
Punctati-sporites auriculaferens (Loose) S. W. & B.

Triangular, 43–53 μ. Tri-radiate mark 2/3 radius. Exospore 1 μ thick with thickened corners; surface sporadically dotted with small warts.

Triquitrites papillosus Knox, nomen nov. Fig. 234. *16K* (Knox, 1948).

Triangular, with sides concave, 40–45 μ. Tri-radiate mark extending almost to the margin. Surface ornamented with small tuberculate processes, 2 μ long and widely spaced, 4–5 μ apart.

Triquitrites spinosus Kosanke Fig. 269.

Radial, trilete; triangular in outline with corners truncate and thickened; 45–55 μ. Tri-radiate mark 2/3 radius. Ornamentation smooth to slightly warty.

This may be conspecific with *T. papillosus* Knox, fig. 234.

Triquitrites tribullatus (Ibr.) S. W. & B. Fig. 270.

Triangular, 42–62 μ. Tri-radiate mark 2/3 radius. Exospore 1 μ thick, increased at the corners to 12 μ broad.

Probably equivalent to *D7* (Raistrick).

Triquitrites trigonappendix (Loose) S. W. & B. Fig. 271.

Triangular, 40–42 μ. Tri-radiate mark 1/3 radius. Bell-shaped outline, with appendages resembling ears at the corners, which are rolled inwards. Surface smooth.

Triquitrites triturgidus (Loose) S. W. & B. Fig. 272.

Triangular, trefoil-shaped; 45–65 μ. Tri-radiate mark 2/3 radius. Corners 10 μ thick; exospore smooth.

Probably equivalent to *D10* (Raistrick).

GENUS X. LYCOSPORA S. W. & B.

Spores radial, trilete; circular or broadly triangular in transverse plane; lenticular in lateral profile, equator marked by a thick tapering ridge. Size 18–45 μ. Ornamentation smooth to granular or rugose.

Key to the Species.

A. Spore diameter greater than 30 μ.	
B. Equatorial wing 6 μ wide	*L. pellucidus*, fig. 276
BB. Equatorial wing 3–4 μ wide . . .	*L. pusillus*, fig. 277
AA. Spore diameter less than 30 μ.	
B. Spore diameter 20–26 μ; exospore papillate .	*L. minutus*, fig. 275
BB. Spore diameter 15–16 μ; exospore micropapillate	*L. micropapillatus*, fig. 274

Lycospora micropapillatus (Wilson & Coe) S. W. & B. Fig. 274.

Tri-radial, with equatorial flange. Body triangular, 15–16 μ. Tri-radiate mark crosses the equatorial flange. Exine micropapillate.

Lycospora minutus (Wilson & Coe) S. W. & B. Fig. 275.

Tri-radial, with equatorial flange; 20–26 μ. Inner edge of flange with a somewhat irregular layer; embedded in this is a series of blunt rods at right angles and surrounding the body of the microspore. Surface papillate.

Lycospora pellucidus (Wicher) S. W. & B. Fig. 276.

Round to oval, with equatorial flange; 30–40 μ. Tri-radiate mark with ridges. Equatorial wing 6 μ wide. Surface microreticulate to punctate.

Lycospora pusillus (Ibr.) S. W. & B. Fig. 277.

Round to oval, 30–40 μ. Tri-radiate mark extending to the margin. Equatorial flange 3–4 μ wide; exospore granular to finely reticulate.

Probably equivalent to *D1* (Raistrick).

GENUS XI. CIRRATRIRADITES Wilson and Coe, 1940.

Spores trilete, radially symmetrical; round to triangular, with a strongly projecting equatorial flange. Size 30–120 μ. Ornamentation may be granular or punctate; the flange may be radially striated and, in addition, may develop one or two concentric bands of irregular thickening.

Key to the Species.

A. Equatorial wing less than 10 μ broad.	
B. Wing smooth.	
C. Exospore smooth	*C. penningtonensis*, fig. 284
CC. Exospore rough	*C. peacocki*, fig. 283
BB. Wing not smooth.	
C. Spore diameter greater than 50 μ	*C. cicatricosus*, fig. 279
CC. Spore diameter less than 50 μ.	
D. Wing punctate	*C. argutus*, fig. 278
DD. Wing faintly reticulate	*C. faunus*, fig. 280
AA. Equatorial wing more than 10 μ broad.	
B. Wing more than 20 μ broad.	
C. Spore diameter less than 60 μ	*C. striatus*, fig. 289
CC. Spore diameter greater than 60 μ.	
D. Tri-radiate mark extending to the margin of the wing, which is striated	*C. aligerens*, fig. 288
DD. Tri-radiate mark extending to the margin of the spore body; wing smooth	*C. carnosus*, fig. 290

BB. Wing less than 20 μ broad.
  C. Spore diameter less than 66 μ.
    D. Wing micro-reticulate . . . . . *C. rarus*, fig. 285
    DD. Wing striated, with a dark inner edge . *C. tenuis*, fig. 287
  CC. Spore diameter greater than 66 μ.
    D. Tri-radiate ridge extending to the margin of the wing . . . . . . *C. maculatus*, fig. 282
      C. saturni, fig. 286
    DD. Tri-radiate ridge extending to the margin of the spore body . . . . *C. formosus*, fig. 281

Cirratriradites aligerens Knox, nom. nov. Fig. 288. *A7* (Raistrick).

Sub-triangular, with a thin membranous equatorial wing; total diameter 70–90 μ. Tri-radiate mark extending to the margin. Surface of spore body granular; wall 5 μ thick; equatorial wing with radial striations.

Cirratriradites argutus (Ibr.) S. W. & B. Fig. 278.

Circular, with an equatorial wing, 46 μ. Tri-radiate mark extending to the margin of the spore body. Surface smooth to punctate.

Cirratriradites carnosus Knox, nom. nov. Fig. 290. *C6* (Knox, 1942 = Millott, 1, 1938).

Sub-triangular to round, 100–120 μ. Tri-radiate mark extending to the margin of the spore body. Surface smooth; wing 20–30 μ broad, with sinuous edge.

Cirratriradites cicatricosus (Ibr.) S. W. & B. Fig. 279.

Spherical, with an equatorial flange, 62–73 μ. Tri-radiate mark extending to the margin. Surface ornamented with irregular ridges, partly toothed; flange 3–4 μ broad, with crenate margin.

Cirratriradites faunus (Ibr.) S. W. & B. Fig. 280.

Spherical, with an equatorial flange, 38–54 μ. Tri-radiate mark 2/3 radius or extending to the margin. Surface punctate or faintly reticulate; flange darker than the centre, 6–8 μ broad, appears faintly reticulate.

Cirratriradites formosus (Ibr.) S. W. & B. Fig. 281.

Round to triangular, with an equatorial flange; 90–95 μ. Tri-radiate mark extending to the margin. Surface faintly reticulate to punctate.

Cirratriradites maculatus Wilson & Coe Fig. 282.

Tri-radial, triangular, 87–89 μ. Tri-radiate ridges cross the equatorial flange.

Cirratriradites peacocki Berry Fig. 283.

Roundly triangular, 31 μ. Tri-radiate mark 2/3 radius. Surface rough or slightly reticulate; central part surrounded by a clear wing, narrow at the angle, wider at sides.

Cirratriradites penningtonensis (Berry) S. W. & B. Fig. 284.

Round, with a narrow keel-like wing, 40–44 μ. Tri-radiate mark extending to the wing. Surface smooth.

Cirratriradites rarus (Ibr.) S. W. & B. Fig. 285.

Circular to triangular, with equatorial flange, 60 μ. Tri-radiate mark extending to the margin. Spore 25 μ, finely reticulate; wing 14–17 μ, finely notched.

Cirratriradites saturni (Ibr.) S. W. & B. Fig. 286.

Round to triangular, with equatorial flange, 66–108 μ. Tri-radiate mark extending to the margin, with ridges or flanges; a characteristic central ring around the points of intersection of the rays. Surface reticulate to punctate.

Probably equivalent to *C5* (Raistrick).

This may be conspecific with *C. formosus* Ibr.

Cirratriradites striatus Knox, nom. nov. Fig. 289. *A9* (Raistrick).

Sub-triangular to round, 50–60 μ. Tri-radiate mark not recorded. Surface granular; central area has a thickened edge; wing 20 μ, radially striated and wrinkled; margin notched.

Cirratriradites tenuis (Loose) S. W. & B. Fig. 287.

Round to oval or polygonal, with an equatorial flange, 42–66 μ. Tri-radiate mark extending to the margin. Surface reticulate. An equatorial ridge, 6–8 μ, supports the equatorial wing by means of struts in the form of fine ridges.

Probably equivalent to *A3* (Raistrick).

Genus XII. Alisporites Daugherty, 1941.

Monotypic genus:

Alisporites opii Daugherty. Fig. 12 in S. W. & B.

Spores trilete, radial; spherical with two membranous wings with reticulate markings. Size 100–110 μ.

Genus XIII. Endosporites Wilson and Coe, 1940.

Spores radial, trilete; oval to slightly triangular; spore body enclosed in a thin-walled bladder. Size 60–175 μ. Surface of bladder smooth to granular; a fine-meshed reticulum is commonly present, but this is probably on the inside of the bladder; spore body smooth.

Key to the Species.

A. Bladder surface reticulate	*E. globiformis*, fig. 292 *E. volans*
AA. Bladder surface not reticulate; usually granulose.	
B. Total spore diameter greater than 140 μ	*E. angulatus*, fig. 291
BB. Total spore diameter less than 140 μ.	
C. Wing less than 10 μ wide	*E. rugatus*, fig. 294 *E. rotundus*
CC. Wing more than 10 μ wide.	
D. Wing with a dark outer rim	*E. zonalis*, fig. 295
DD. Wing without a dark outer rim	*E. ornatus*, fig. 293 *E. pellucidus*

Endosporites angulatus Wilson & Coe Fig. 291.

Sub-triangular, 145–175 μ. Spore body 75–85 μ. Wall thin and transparent; outer wall granulose.

Endosporites globiformis (Ibr.) S. W. & B. Fig. 292. *3K* (Knox, 1942).

Spherical, 90–140 μ. Spore body 50–60 μ. Tri-radiate mark extending to the margin of the spore body. Wing, 25–35 μ, faintly reticulate, with margin toothed.

Endosporites ornatus Wilson & Coe Fig. 293.

Spherical, 91–113 μ. Tri-radiate mark extending to the margin of spore body. Wall thin, transparent and granulose. Spore body 47–54 μ.

Endosporites pellucidus Wilson & Coe

Similar to *E. ornatus* but smaller. Diameter 47–57 μ; spore body 25–36 μ.

Endosporites rotundus (Ibr.) S. W. & B.

Spherical, 63–81 μ. Tri-radiate mark extending to the margin of the spore body. Surface of bladder punctate; margin smooth.

Endosporites rugatus (Ibr.) S. W. & B. Fig. 294. *46K* (Knox, 1948).

Spherical, 77–80 μ. Tri-radiate mark 1/3 radius. Wing 6–8 μ broad, punctate.

Endosporites volans (Loose) S. W. & B.

Oval to round, 74–140 μ. Tri-radiate mark faint and small. Surface of bladder faintly reticulate.

Endosporites zonalis (Loose) Knox, comb. nov. Fig. 295.
Cirratriradites zonalis (Loose) S. W. & B.

Spherical to sub-triangular, 75–100 μ. Tri-radiate mark extending to the margin, indistinct. Spore body 48–68 μ, with wing 6–8 μ wide; surface of wing faintly reticulate; wing strengthened round its margin.

Probably equivalent to *C1* (Raistrick).

GENUS XIV. CALAMOSPORA S. W. & B.

Spores trilete, radial; spherical or nearly so; 40 μ to several hundred microns. Spore coat usually thin and smooth to slightly granular or rugose; often much folded.

Key to the Species.

A. Spore diameter less than 40 μ	*C. minutus*, fig. 301
AA. Spore diameter greater than 40 μ.	
B. Exospore smooth.	
C. Wall 5–7 μ thick	*C. obesus*, fig. 299 *C. laevigatus*
CC. Wall thin and much folded	*C. microrugosus*, fig. 297 *C. mutabilis*, fig. 298 *C. perrugosus*
BB. Exospore granulose.	
C. Spore oval	*C. pallidus*, fig. 300
CC. Spore spherical	*C. Hartungiana*, fig. 296

Calamospora Hartungiana Schopf Fig. 296.

Spherical, 80–100 μ. Tri-radiate mark 1/3 radius. Spore coat thin, minutely granular and folded.

Calamospora laevigatus (Ibr.) S. W. & B.

Oval to spherical, 260–300 μ. Tri-radiate mark 1/3 radius. Exospore up to 7 μ thick; smooth and folded.

Calamospora microrugosus (Ibr.) S. W. & B. Fig. 297.

Polygonal to round, 58–90 μ. Tri-radiate mark 2/3 radius. Exospore smooth and almost always folded.

Calamospora minutus Knox, nom. nov. Fig. 301. *B7* (Raistrick).

Spherical, 25–35 μ. Tri-radiate mark extending almost to the margin. Exospore thin and smooth.

Calamospora mutabilis (Loose) S. W. & B. Fig. 298.

Oval to round, 63–126 μ. Tri-radiate mark 2/3 radius. Exospore smooth.

Probably equivalent to *B3* (Raistrick).

Calamospora obesus (Loose) S. W. & B. Fig. 299.

Spherical to ovoid, 97–160 μ. Tri-radiate mark 1/3 radius. Exospore 5 μ thick, smooth to punctate or faintly reticulate.

Probably equivalent to *7K* (Knox, 1942, fig. 4).

Calamospora pallidus (Loose) S. W. & B. Fig. 300.

Oval to polygonal, 67 × 58 – 54 × 47 μ. Tri-radiate mark 2/3 radius. Exospore faintly punctate to slightly rough.

Calamospora perrugosus (Loose) S. W. & B.

Oval to round, 122–155 μ. Tri-radiate mark 2/3 radius. Exospore smooth and folded. Similar to *C. mutabilis*.

Genus XV. Reinschospora S. W. & B.

Spores radial, trilete; sub-triangular in transverse plane with rounded corners. A fimbriate flange may be present to modify the marginal outline. Size 30–85 μ. Spore body smooth to granular. Flange closely striate to fimbriate, sometimes so incised as to form a row of apiculae.

Reinschospora bellitas Bentall. Fig. 2, S. W. & B.

Sub-triangular, 57–76 μ. Tri-radiate mark extending almost to the margin. Flange fimbriate.

Reinschospora speciosa (Loose) S. W. & B.

Triangular, trefoil-shaped, 50–55 μ. Tri-radiate mark extending to the margin. Exospore smooth; three wings with radial rays up to 20 μ in width on sides of the spore body.

Genus XVI. Raistrickia S. W. & B.

Spores radial, trilete; spherical to sub-triangular. Size 40–90 μ. Ornamentation verrucose or spinose; spines truncate and blunt-tipped. The spine tips may be dissected into two to six terminal papillae.

Key to the Species.

A. Processes 4–8 μ in length.	
B. Spore diameter greater than 50 μ . . .	*R. saetosus*, fig. 304
BB. Spore diameter less than 50 μ; wall 3–4 μ thick .	*R. superbus*, fig. 306
AA. Processes less than 4 μ long.	
B. Processes thin, 1 –3 μ	*R. spinososaetosus*, fig. 305
BB. Processes 2–5 μ broad.	
C. Processes 3–5 μ long	*R. grovensis*, fig. 303
CC. Process 2–4 μ long	*R. fibratus*, fig. 302

Raistrickia fibratus (Loose) S. W. & B. Fig. 302.

Spherical, 46–58 μ. Tri-radiate mark 2/3 radius. Exospore ornamented with fibrous bristles from 2 μ broad to 2–4 μ long.

Probably equivalent to *E3* (Raistrick).

Raistrickia grovensis Schopf Fig. 303.

Rounded triangular, 50 μ. Tri-radiate mark 1/3 radius. Surface ornamented with numerous short, 3–5 μ long and 2–4 μ broad, blunt-tipped spines which sometimes appear mutually attached.

Raistrickia saetosus (Loose) S. W. & B. Fig. 304.

Oval to round, 50–93 μ. Tri-radiate mark 2/3 radius. The surface is beset with numerous processes, 4–8 μ long and 2–6 μ broad.

Raistrickia spinososaetosus (Loose) S. W. & B. Fig. 305.

Oval to round, 45–75 μ. Tri-radiate mark 2/3 radius. Surface ornamented with processes 1·5–4 μ long and 1–3 μ broad.

Raistrickia superbus (Ibr.) S. W. & B. Fig. 306.

Ovoid, 46–54 μ. Tri-radiate mark extending to the margin. Spines 4–8 μ long and 2–4 μ broad. Exospore 3–4 μ thick.

GENUS XVII. FLORINITES S. W. & B.

Spores apparently bilateral; spore body spherical, nearly enclosed by a bladder giving a broadly elliptical outline. Size 50–180 μ. Ornamentation of the exterior surface smooth or finely granular; internally the membrane bears a distinct reticulum.

Florinites antiqua Schopf Fig. 4. S. W. & B., p. 59.

"Pollen grains" with bilateral symmetry, with an annulate bladder joined to the central body only on the distal side. The grains are broadly elliptical. Size inclusive of the bladder from 55 to 90 μ in length and 40 to 75 μ broad. The body is almost spherical, 25–45 μ. The bladder is smooth to granular, with an internal reticulation, 1–3 μ; the body wall is thin and smooth.

Florinites pumicosus (Ibr.) S. W. & B.

Oval to round, 62–92 μ. Surface micro-reticulate, and reticulation indistinct in the centre.

Florinites visendus (Ibr.) S. W. & B.

Ovate to round, 115–175 μ. Spore body with a wing which is micro-reticulate. Reticulation in the centre of the spore is faint.

This spore is similar to *3K* (Knox, 1942, fig. 4) and to *Endosporites globiformis* (fig. 292).

COMPARISON OF PALAEOZOIC SPORES WITH THOSE OF LYCOPODIUM, SELAGINELLA AND ISOETES.

It is now possible to make certain generalisations and comparisons between the genera of Palaeozoic spores and the groups of spore types in the genera Lycopodium, Selaginella and Isoetes.

Indications have been given in the preceding pages that the spore ornamentation in the *Lycopodiaceae* and *Selaginellaceae* bears a striking resemblance in many instances to that of isolated fossil spores from plant-bearing strata of the Palaeozoic.

The reticulate or pitted nature of the exospore in the genus Lycopodium is an acknowledged fact; in all probability, therefore, a large proportion of the fossil spores assigned to the genera *Microreticulati-sporites* and *Reticulati-sporites* are of Lycopodean affinity, with the possible exception of *Reticulati-sporites polygonalis* (fig. 255) and *Reticulati-sporites fimbriatus* (fig. 257); ornamentation of the spores of the latter resemble closely the sculpturing seen in *Selaginella Willdenovii* (fig. 95). The Palaeozoic genus Triquitrites recalls the spores of the group of *Lycopodium Selago* (figs. 1–6) in shape and in the thickened, truncate corners, though lacking the pitted exospore characteristic of the living species.

The microspores of the *Selaginellaceae* are divisible into two main series: (1) those with a membranous wing or annular ring; and (2) those without a wing but furnished with excrescences varying in shape, size and disposition.

The comparable fossil spores possessing a thin encircling bladder are classed together in the genus Endosporites; some members of this genus closely resemble species included in the group of *Selaginella sibirica*—e.g. *Endosporites rugatus* (fig. 294), though larger, is otherwise similar to *S. strutholoides* (fig. 79), while *Endosporites angulatus* and *Endosporites zonalis* (figs. 291 and 295) recall *S. Wallacei* (fig. 81).

The spores of Selaginella which have an annular ring (group of *S. scandens*, figs. 98–101), and those with an equatorial flange (group of *S. sanguinolenta*, figs. 83–89), have both their counterparts in the Palaeozoic genera of Denso-sporites (figs. 265-267) and Cirratriradites (figs. 278–290) respectively. The species of Cirratriradites possessing a membranous flange are allied to such types as *S. semicordata*, *S. Mayeri* and others of the group of *S. megastachys* (figs. 97, 90 and 96).

Close parallels can also be cited between Palaeozoic spores and spores of living representatives of *Selaginellaceae*, in which the exospore exhibits either spines, tubercles or rod-like processes. The resemblances are too many to quote here; suffice to indicate the similarities of fossil genera to spore groups.

Spinoso-sporites, with ornamentation of pointed processes, corresponds to Groups XV–XVIII, *i.e.* the groups of *S. subarborescens*, *S. anceps*, *S. uncinata* and *S. magnifica*.

Plani-sporites, with smooth or granular spores, corresponds to Groups V–VII, *i.e.* the groups of *S. firmula*, *S. helvetica* and *S. cathedrifolia*.

Verrucoso-sporites, with ornamentation of rounded, warty or tuberculate processes, corresponds to Groups VIII–X, *i.e.* the groups of *S. radicata*, *S. leptophylla* and *S. vaginata*.

Raistrickia, with blunt, straight-sided processes, corresponds to Groups XIII and XIV, *i.e.* the groups of *S. biformis* and *S. latifrons*.

Of the remaining genera of Palaeozoic spores, the bilateral, monolete Laevigato-sporites forms are probably of Filicean affinity, though a few may be related to *Isoetaceae*. The large, thin-walled, spherical, unornamented types of the genus Calamospora are almost certainly Calamarian; Alisporites, Florinites and some species of Endosporites are known to be related to Cordaianthus and Caytonanthus. They thus represent "a part of the upper Palaeozoic gymnospermic alliance" (Schopf, 1944).

Whilst many fossil spores may be related to the Lycopodinean families, it must not be forgotten that close parallels can also be drawn with spores of the Hepaticae (Knox, 1939); and it is not unlikely that Bryophytic plants contributed their share to the formation of the coal swamps (Walton, 1925, 1928).

It is important to realise that evolutionary convergence as well as community of derivation account for the recurrence of similar specific features in spore morphology in different phyla and in different geologic periods. Consequently the relationship of isolated fossil spores to the parent stock can only be hinted at; only as microfossils are found in organic connection with a known species can any certainty of lineage be maintained.

The suggestions put forward are therefore purely tentative; not until our knowledge of the fossil flora is greatly increased can positive assertions be made; time alone can prove the correctness of our judgments and the veracity of our theories.

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EXPLANATION OF PLATES.

In figures 1–197 the magnification is ×450; in figures 198–306 the magnification is ×250.

Ap. = apical view. Ab-ap. = ab-apical view. l. = lateral view.

PLATE VIII. LYCOPODIACEAE.

Spores of *Lycopodium Selago* group (figs. 1–6).

FIG.
1 *a*. *L. Selago* L. (ab-ap.)
1 *b*. *L. Selago* (ap.)
2. *L. fontinaloides* Spring (ap.)
3 *a*. *L. serratum* Thunb. (ap.)
3 *b*. *L. serratum* (ab-ap.)
4. *L. miniatum* Spring (ab-ap.)
5. *L. ceylanicum* Spring (ap.)
6. *L. lucidulum* Michx. (ap.)

Spores of *Lycopodium Phlegmaria* group (figs. 7–30).

FIG.
7. *L. Sieboldi* Miquel. (ab-ap.)
8. *L. robustum* Klotzsch (ab-ap.)
9. *L. aqualupianum* Spring (ap.)
10. *L. callitrichaefolium* Mett. (ab-ap.)
11. *L. carinatum* Desv. (ab-ap.)
12. *L. casuarinoides* Spring (ap.)
13. *L. cryptomerinum* Maxim. (ap.)
14. *L. Dalhousianum* Spring (ap.)
15. *L. erythraeum* Spring (ab-ap.)
16. *L. Hamiltonii* Spring (ab-ap.)
17. *L. mollicomum* Mart. (ap.)
18. *L. myrsinites* Lam. (ab-ap.)
19 *a*. *L. Phlegmaria* L. (ab-ap.)
19 *b*. *L. Phlegmaria* (ap.)
20. *L. sarmentosum* Spring (ap.)
21. *L. dichotomum* Jacq. (ap.)
22. *L. firmum* Mett. (ap.)
23. *L. Lindeni* Spring (ap.)
24. *L. megastachyum* Baker (ap.)
25. *L. Saururus* Lam. (ap.)
26. *L. compactum* Hook. (ap.)
27. *L. Jamesoni* Baker (ab-ap.)
28. *L. obtusifolium* Sw. (ap.)
29. *L. reflexum* Lam. (ap.)
30. *L. tetragonum* Hk. & Gr. (ap.)

PLATE IX. LYCOPODIACEAE.

Spores of *Lycopodium Phlegmaria* group (*contd.*) (figs. 31–43).

FIG.	
31.	*L. affine* Hk. & Gr. (ap.)
32.	*L. echinatum* Spring (ap.)
33.	*L. gnidioides* L. (ap.)
34.	*L. myrtuosum* Spring (ap.)
35.	*L. rufescens* Hook. (ap.)
36.	*L. setaceum* Hamilt. (ab-ap.)
37.	*L. subulatum* Desv. (ap.)
38.	*L. Billardieri* Spring (ab-ap.)
39.	*L. cancellatum* Spring (ab-ap.)
40.	*L. insulare* Carm. (ab-ap.)
41.	*L. nummularifolium* Blume (ap.)
42 *a*.	*L. Pearcei* Baker (ab-ap.)
42 *b*.	*L. Pearcei* (ap.)
43.	*L. pinifolium* Blume (ab-ap.)

Spores of *Lycopodium verticillatum* group (figs. 44–48).

FIG.	
44.	*L. taxifolium* Sw. (ap.)
45.	*L. verticillatum* L. (ap.)
46.	*L. polytrichoides* Kaulf. (ap.)
47.	*L. rubrum* Chamisso (ap.)
48.	*L. xiphophyllum* Baker (ap.)

Spores of *Lycopodium clavatum* group (figs. 49–55).

FIG.	
49.	*L. diaphanum* Sw. (ab-ap.)
50 *a*.	*L. contiguum* Klotzsch (ab-ap.)
50 *b*.	*L. contiguum* (ap.)
51.	*L. Wightianum* Wall. (ab-ap.)
52.	*L. scariosum* Forst. (ab-ap.)
53 *a*.	*L. vestitum* Desv. (ab-ap.)
53 *b*.	*L. vestitum* (ap.)
54.	*L. volubile* Forst. (l.)
55 *a*.	*L. annotinum* L. (ap.)
55 *b*.	*L. annotinum* (ab-ap.)

PLATE X.

Spores of *Lycopodium clavatum* group (figs. 56–60).

FIG.	
56 *a*.	*L. laterale* R. Br. (ap.)
56 *b*.	*L. laterale* (ab-ap.)
57 *a*.	*L. magellanicum* Sw. (ab-ap.)
57 *b*.	*L. magellanicum* (ap.)
58.	*L. ramulosum* Kirk (l.)
59.	*L. Sprucei* Baker (l.)
60 *a*.	*L. alpinum* L. (ab-ap.)
60 *b*.	*L. alpinum* (ap.)

Spores of *Lycopodium clavatum* group (*contd.*) (figs. 61–74).

FIG.

61 *a.* *L. clavatum* L. (ab-ap.)
61 *b.* *L. clavatum* (ap.)
62 *a.* *L. paniculatum* Desv. (ap.)
62 *b.* *L. paniculatum* (ab-ap.)
63 *a.* *L. complanatum* L. (ap.)
63 *b.* *L. complanatum* (ab-ap.)
64 *a.* *L. adpressum* Champ. (ap.)
64 *b.* *L. adpressum* (l.)
65 *a.* *L. cernuum* L. (ap.)
65 *b.* *L. cernuum* (ab-ap.)
66. *L. phyllanthum* Hook. & Arn. (ab-ap.)
67. *Phylloglossum Drummondii* Kunze (ab-ap.)
68. *L. spurium* Willd. (l.)
69 *a.* *L. obscurum* L. (l.)
69 *b.* *L. obscurum* (ab-ap.)
70. *L. Drummondii* Spring (ap.)
71 *a.* *L. inundatum* L. (ap.)
71 *b.* *L. inundatum* (ab-ap.)
72 *a.* *L. fastigiatum* R. Br. (ap.)
72 *b.* *L. fastigiatum* (ab-ap.)
73. *L. diffusum* R. Br. (ap.)
74 *a.* *L. carolinianum* L. (ab-ap.)
74 *b.* *L. carolinianum* (ap.)
75 *a.* *L. densum* La Billard (ab-ap.)
75 *b.* *L. densum* (l.)

PLATE XI. SELAGINELLACEAE.

Spores of *S. sibirica* group (figs. 76–82).

FIG.

76. *S. uliginosa* Spring (ap.)
77. *S. sibirica* (Milde) Hieron. (ap.)
78. *S. arenicola* Underw. (ap.)
79. *S. strutholoides* (Presl.) Underw. (ap.)
80. *S. pygmaea* Kaulf. (ap.)
81. *S. Wallacei* Hieron. (ap.)
82. *S. Preissiana* Spring (ap.)

Spores of *S. sanguinolenta* group (figs. 83–89).

FIG.

83 *a.* *S. laevigata* Baker (ap.)
83 *b.* *S. laevigata* (l.)
84 *a.* *S. valdepilosa* Baker (ap.)
84 *b.* *S. valdepilosa* (l.)
85. *S. saccharata* A. Br. (ap.)
86. *S. sanguinolenta* (L.) Spring (ap.)
87. *S. borealis* Spring (l.)
88 *a.* *S. pedata* Klotzsch (ap.)
88 *b.* *S. pedata* (l.)
89 *a.* *S. stenophylla* A. Br. (ab-ap.)
89 *b.* *S. stenophylla* (l.)

PLATE XII. SELAGINELLACEAE.

Spores of *S. megastachys* group (figs. 90–97).

FIG.

90 *a*. *S. Mayeri* Hieron. (ap.)
90 *b*. *S. Mayeri* (ab-ap.)
91 *a*. *S. tylophora* vA. vR. (ap.)
91 *b*. *S. tylophora* (ab-ap.)
92 *a*. *S. integerrima* Spring (l.)
92 *b*. *S. integerrima* (ap.)
93. *S. asperula* vA. vR. (ap.)
94. *S. flaccida* Spring (l.)
95. *S. Willdenovii* Baker (ab-ap.)
96 *a*. *S. megastachys* Baker (ap.)
96 *b*. *S. megastachys* (ab-ap.)
97 *a*. *S. semicordata* Spring (ap.)
97 *b*. *S. semicordata* (ab-ap.)

Spores of *S. scandens* group (figs. 98–101).

FIG.

98 *a*. *S. puberula* Spring (l.)
98 *b*. *S. puberula* (ap.)
99 *a*. *S. scandens* Spring (l.)
99 *b*. *S. scandens* (ap.)
100 *a*. *S. stellata* Spring (ap.)
100 *b*. *S. stellata* (l.)
101 *a*. *S. Parkeri* Spring (ap.)
101 *b*. *S. Parkeri* (l.)

PLATE XIII. SELAGINELLACEAE.

Spores of *S. firmula* group (figs. 102–109).

FIG.

102. *S. cordifolia* Spring (ap.)
103. *S. firmula* A. Br. (ap.)
104. *S. Volkensii* Hieron. (ap.)
105. *S. Roxburghii* (Hk. & Gr.) Spring (ap.)
106. *S. Hochreutineri* Hieron. (ap.)
107. *S. nana* (Desv.) Spring (ap.)
108. *S. Burbidgei* Baker (ap.)
109. *S. marginata* Spring (ap.)

Spores of *S. helvetica* group (figs. 110–115).

FIG.

110. *S. Whitmeei* Baker (ap.)
111. *S. helvetica* Link (ap.)
112. *S. Kernbachii* Hieron (ap.)
113. *S. philippina* Spring (ap.)
114. *S. megaphylla* Baker (ap.)
115. *S. arbuscula* Spring (ap.)

Spores of *S. cathedrifolia* group (figs. 116–122).

FIG.	
116.	*S. tamariscina* (Beauv.) Spring (ap.)
117 *a*.	*S. cathedrifolia* Spring (ap.)
117 *b*.	*S. cathedrifolia* (l.)
118.	*S. producta* Baker (ap.)
119.	*S. heterostachys* Baker (ap.)
120.	*S. falcata* Spring (ap.)
121.	*S. Savatieri* Baker (ap.)
122.	*S. platybasis* Baker (ap.)

Spores of *S. radicata* group (figs. 123–131).

FIG.	
123 *a*.	*S. apus* Spring (ap.)
123 *b*.	*S. apus* (ab-ap.)
124.	*S. Ludoviciana* A. Br. (ap.)
125.	*S. velutina* Cesati (ap.)
126.	*S. pallidissima* Spring (ap.)
127.	*S. Balfouri* Baker (ap.)
128.	*S. abyssinica* Spring (ap.)
129.	*S. radicata* (Hk. & Gr.) Spring (ap.)
130.	*S. sub-diaphana* (Wall.) Spring (ap.)
131.	*S. tenera* (Hk. & Gr.) Spring (ab-ap.)

Spores of *S. leptophylla* group (figs. 132–135).

FIG.	
132.	*S. pentagona* Spring (ab-ap.)
133.	*S. effusa* Alston (ap.)
134.	*S. ciliaris* (Retz.) Spring (ab-ap.)
135.	*S. leptophylla* Baker (ap.)

PLATE XIV. SELAGINELLACEAE.

Spores of *S. vaginata* group (figs. 136–140).

FIG.	
136.	*S. Mettenii* A. Br. (ap.)
137.	*S. tenuifolia* Spring (ab-ap.)
138.	*S. opaca* Warb. (ab-ap.)
139.	*S. sinensis* (Desv.) Spring (ab-ap.)
140 *a*.	*S. vaginata* Spring (ab-ap.)
140 *b*.	*S. vaginata* (ap.)

Spores of *S. repanda* group (figs. 141–143).

FIG.	
141.	*S. Beccariana* Baker (ab-ap.)
142.	*S. calcicola* Hieron. (ap.)
143 *a*.	*S. repanda* (Desv.) Spring (ab-ap.)
143 *b*.	*S. repanda* (ap.)

Spores of *S. stolonifera* group (figs. 144–150).

FIG.
144. *S. Hookeri* Baker (ap.)
145. *S. monospora* Spring (ab-ap.)
146. *S. permutata* Hieron. (l.)
147. *S. polystachya* (Warb.) Hieron. (ap.)
148. *S. inaequalifolia* (Hk. & Gr.) Spring (ab-ap.)
149. *S. stolonifera* Spring (ab-ap.)
150. *S. conferta* Baker (ab-ap.)

Spores of *S. biformis* group (figs. 151–157).

FIG.
151. *S. intermedia* (Bl.) Spring (ab-ap.)
152. *S. caulescens* (Wall.) Spring (ap.)
153 *a*. *S. haematodes* Spring (ab-ap.)
153 *b*. *S. haematodes* (l.)
154. *S. ascendens* vA. vR. (ab-ap.)
155. *S. frondosa* Warb. (l.)
156. *S. biformis* A. Br. (ab-ap.)
157. *S. trachyphylla* A. Br. (l.)

Spores of *S. latifrons* group (figs. 158–162).

FIG.
158. *S. atroviridis* Spring (ab-ap.)
159. *S. sumatrana* Hieron. (l.)
160. *S. longipinna* Warb. (l.)
161. *S. latifrons* Warb. (l.)
162. *S. denudata* Spring (ab-ap.)

PLATE XV. SELAGINELLACEAE.

Spores of *S. sub-arborescens* group (figs. 163–167).

FIG.
163 *a*. *S. sub-arborescens* Hook. (ab-ap.)
163 *b*. *S. sub-arborescens* (l.)
164. *S. Elmeri* Hieron. (ab-ap.)
165. *S. cupressina* A. Br. (ab-ap.)
166. *S. erectifolia* Spring (l.)
167. *S. peltata* Presl. (ab-ap.)

Spores of *S. anceps* group (figs. 168–172).

FIG.
168. *S. Wallichii* Spring (ab-ap.)
169. *S. anceps* Presl. (ab-ap.)
170. *S. erythropus* (Mart.) Spring (l.)
171 *a*. *S. blepharostachys* Alston (ab-ap.)
171 *b*. *S. blepharostachys* (ap.)
172. *S. Mayerhoffii* Hieron. (ab-ap.)

Spores of *S. uncinata* group (figs. 173–180).

FIG.	
173.	*S. Eggersii* Sodiro (ab-ap.)
174.	*S. intacta* Baker (ap.)
175.	*S. articulata* Spring (ab-ap.)
176.	*S. bombycina* Spring (ap.)
177 *a*.	*S. uncinata* Spring (ab-ap.)
177 *b*.	*S. uncinata* (ap.)
178.	*S. chilensis* Spring (ab-ap.)
179.	*S. geniculata* Spring (ap.)
180.	*S. Poeppigiana* Spring (ab-ap.)

Spores of *S. magnifica* group (figs. 181–185).

FIG.	
181.	*S. cagayanensis* Hieron. (ab-ap.)
182.	*S. Spanielema* Alston (ab-ap.)
183.	*S. Brooksii* Hieron. (l.)
184.	*S. magnifica* Warb. (ab-ap.)
185.	*S. alligans* Hieron. (l.)

Spores of *S. selaginoides* group (figs. 186, 187).

FIG.	
186 *a*.	*S. selaginoides* Link (ap.)
186 *b*.	*S. selaginoides* (ab-ap.)
187.	*S. atirrensis* Hieron. (ab-ap.)

Spores of *S. Kraussiana* group (figs. 188, 189).

FIG.	
188.	*S. Kraussiana* A. Br. (ap.)
189.	*S. Kunzeana* A. Br. (ab-ap.)

PLATE XVI. ISOETACEAE.

Spores of *I. echinospora* group (figs. 190–191).

FIG.	
190 *a*.	*I. Drummondii* A. Br. (l.)
190 *b*.	*I. Drummondii* (ap.)
191 *a*.	*I. echinospora* Dur. (l.)
191 *b*.	*I. echinospora* (ap.)

Spores of *I. adspersa* group (figs. 192–194).

FIG.	
192 *a*.	*I. ovata* Pfeiffer (l.)
192 *b*.	*I. ovata* (ap.)
193 *a*.	*I. Gardneriana* A. Br. (l.)
193 *b*.	*I. Gardneriana* (ap.)
194 *a*.	*I. adspersa* A. Br. (l.)
194 *b*.	*I. adspersa* (ap.)

Spores of *I. Hystrix* group (figs. 195–197).

FIG.	
195.	*I. habbemensis* Alston (l.)
196.	*I. japonica* A. Br. (l.)
197 *a*.	*I. Hystrix* Bory & Dur. (l.)
197 *b*.	*I. Hystrix* (ap.)

Plate XVII. Fossil Spores.

Spores of Spinoso-sporites Knox, gen. nov. (figs. 198–208).

FIG.
198. *S. aculeatus* (Ibr.) Knox, comb. nov.
199. *S. globosus* (Loose) Knox, comb. nov.
200. *S. latigranifer* (Loose) Knox, comb. nov.
201. *S. spinosus* (Loose) Knox, comb. nov.
202. *S. spinulistratus* (Loose) Knox, comb. nov.
203. *S. microsaetosus* (Loose) Knox, comb. nov.
204. *S. microspinosus* (Ibr.) Knox, comb. nov.
205. *S. falcatus* Knox, nom. nov.
206. *S. ciliatus* Knox, nom. nov.
207. *S. denticulatus* Knox, nom. nov.
208. *S. echinatus* Knox, nom. nov.

Spores of Plani-sporites Knox, gen. nov. (figs. 209–223).

FIG.
209. *P. aureus* (Loose) Knox, comb. nov.
210. *P. granifer* (Ibr.) Knox, comb. nov.
211. *P. microtuberosus* (Loose) Knox, comb. nov.
212. *P. parvipunctatus* (Kosanke) Knox, comb. nov.
213. *P. punctatus* (Ibr.) Knox, comb. nov.
214. *P. sphaerotriangulatus* (Loose) Knox, comb. nov.
215. *P. deltiformis* (S. W. & B.) Knox, comb. nov.
216. *P. deltoides* (Ibr.) Knox, comb. nov.
217. *P. granulatus* (Ibr.) Knox, comb. nov.
218. *P. microgranifer* (Ibr.) Knox, comb. nov.
219. *P. piroformis* (Loose) Knox, comb. nov.
220. *P. priddyi* (Berry) Knox, comb. nov.
221. *P. verrucosus* (Wilson & Coe) Knox, comb. nov.
222. *P. ovatus* Knox, nom. nov.
223. *P. crassus* Knox, nom. nov.

Spores of Verrucoso-sporites Knox, gen. nov. (figs. 224–237).

FIG.
224. *V. bucculentus* (Loose) Knox, comb. nov.
225. *V. firmus* (Loose) Knox, comb. nov.
226. *V. grumosus* (Ibr.) Knox, comb. nov.
227. *V. insignitis* (Ibr.) Knox, comb. nov.
228. *V. microverrucosus* (Ibr.) Knox, comb. nov.
229. *V. papillosus* (Ibr.) Knox, comb. nov.
230. *V. verrucosus* (Ibr.) Knox, comb. nov.
231. *V. tuberculatus* (Berry) Knox, comb. nov.
232. *V. gibbosus* (Ibr.) Knox, comb. nov.
233. *V. triquetris* (Ibr.) Knox, comb. nov.
234. *Triquitrites papillosus*, Knox, nom. nov.
235. *V. morulatus* Knox, nom. nov.
236. *V. tuberosus* Knox, nom. nov.
237. *V. maculosus* Knox, nom. nov.

PLATE XVIII. FOSSIL SPORES.

Spores of MICRORETICULATI-SPORITES Knox, gen. nov. (figs. 238–250).

FIG.
238. *M. corrugatus* (Ibr.) Knox, comb. nov.
239. *M. cusus* (Loose) Knox, comb. nov.
240. *M. lacunosus* (Ibr.) Knox, comb. nov.
241. *M. maculatus* (Ibr.) Knox, comb. nov.
242. *M. nobilis* (Wicher) Knox, comb. nov.
243. *M. reticulocingulum* (Loose) Knox, comb. nov.
244. *M. trigonoreticulatus* (Loose) Knox, comb. nov.
245. *M. velatus* (Loose) Knox, comb. nov.
246. *M. fistulosus* (Ibr.) Knox, comb. nov.
247. *M. parvus* (Ibr.) Knox, comb. nov.
248. *M. torquifer* (Loose) Knox, comb. nov.
249. *M. trigonus* (Ibr.) Knox, comb. nov.
250. *M. Thiessenii* (Kosanke) Knox, comb. nov.

Spores of RETICULATI-SPORITES (Ibrahim, 1933) emend., S. W. & B. (figs. 251–257).

FIG.
251. *R. corporeus* Loose
252. *R. facetus* (Ibr.) S. W. & B.
253. *R. mediareticulatus* Ibr.
254. *R. ornatus* (Ibr.) S. W. & B.
255. *R. polygonalis* (Ibr.) S. W. & B.
256. *R. reticuliformis* Ibr.
257. *R. fimbriatus* Knox, nom. nov.

Spore of ALATI-SPORITES Ibrahim, 1933 (fig. 258).

FIG.
258. *A. pustulatus* Ibr.

Spores of LAEVIGATO-SPORITES (Ibrahim, 1933) emend., S. W. & B. (figs. 259–264).

FIG.
259. *L. bilateralis* (Loose) S. W. & B.
260. *L. desmoinensis* (Wilson & Coe), S. W. & B.
261. *L. minimus* (Wilson & Coe) S. W. & B.
262. *L. minutus* (Ibr.) S. W. & B.
263. *L. pennovalis* Berry
264 *a*. *L. vulgaris* Ibr. *forma* major.
264 *b*. *L. vulgaris* Ibr. *forma* minor.

Spores of DENSO-SPORITES (Berry, 1937) emend., S. W. & B. (figs. 265–267).

FIG.
265. *D. annulatus* (Loose) S. W. & B.
266. *D. indignabundus* (Loose) S. W. & B.
267. *D. pannosus* Knox, nom. nov.

Spores of TRIQUITRITES Wilson & Coe, 1940 (figs. 268–273).

FIG.
268. *T. arculatus* Wilson & Coe
269. *T. spinosus* Kosanke
270. *T. tribullatus* (Ibr.) S. W. & B.
271. *T. trigonappendix* (Loose) S. W. & B.
272. *T. triturgidus* (Loose) S. W. & B.
273. *T. auriculaferens* (Loose) Knox, comb. nov.

Spores of LYCOSPORA S. W. & B. (figs. 274–277).

FIG.
274. *L. micropapillatus* (Wilson & Coe) S. W. & B.
275. *L. minutus* (Wilson & Coe) S. W. & B.
276. *L. pellucidus* (Wicher) S. W. & B.
277. *L. pusillus* (Ibr.) S. W. & B.

PLATE XIX. FOSSIL SPORES.

Spores of CIRRATRIRADITES Wilson & Coe, 1940 (figs. 278–290).

FIG.
278. *C. argutus* (Ibr.) S. W. & B.
279. *C. cicatricosus* (Ibr.) S. W. & B.
280. *C. faunus* (Ibr.) S. W. & B.
281. *C. formosus* (Ibr.) S. W. & B.
282. *C. maculatus* Wilson & Coe
283. *C. peacocki* Berry
284. *C. penningtonensis* (Berry) S. W. & B.
285. *C. rarus* (Ibr.) S. W. & B.
286. *C. saturni* (Ibr.) S. W. & B.
287. *C. tenuis* (Loose) S. W. & B.
288. *C. aligerens* Knox, nom. nov.
289. *C. striatus* Knox, nom. nov.
290. *C. carnosus* Knox, nom. nov.

Spores of ENDOSPORITES Wilson & Coe, 1940 (figs. 291–295).

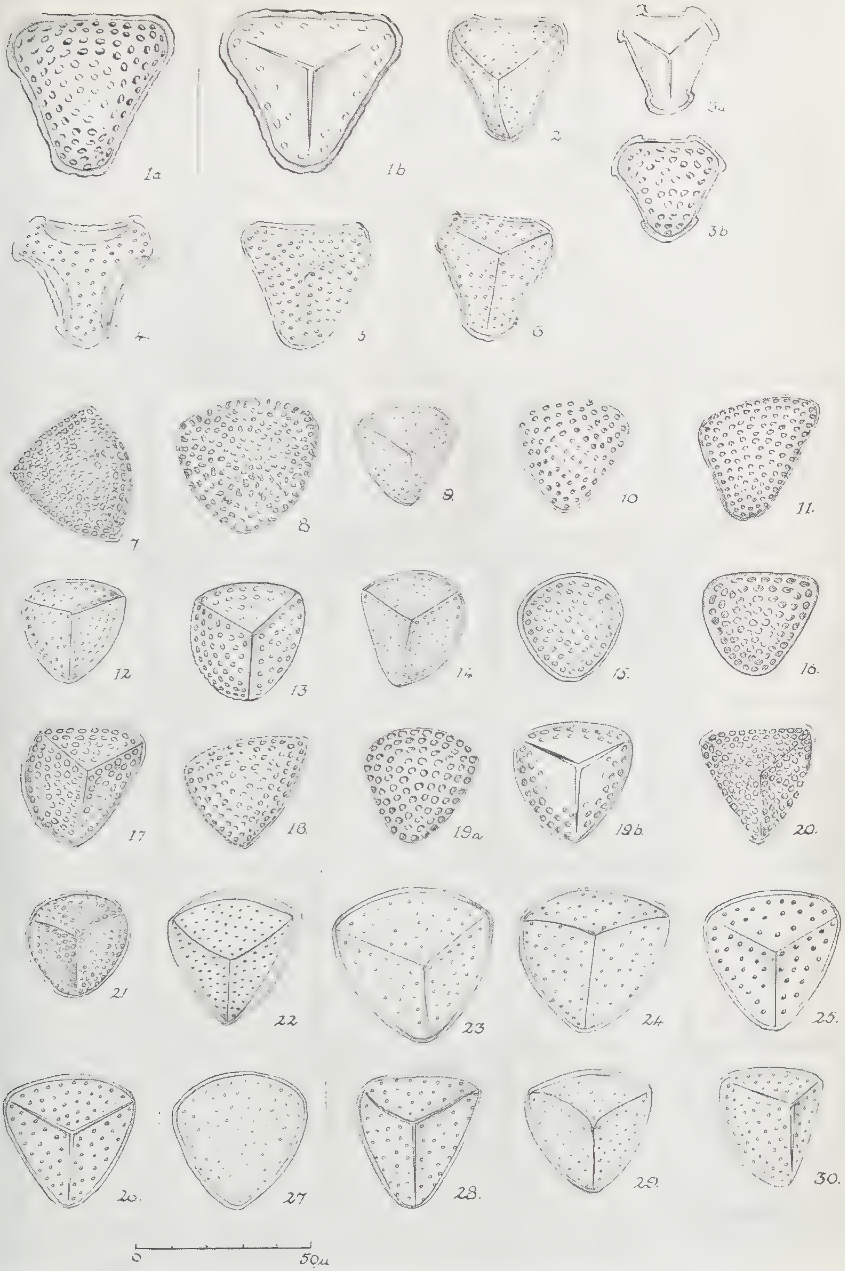
FIG.
291. *E. angulatus* Wilson & Coe
292. *E. globiformis* (Ibr.) S. W. & B.
293. *E. ornatus* Wilson & Coe
294. *E. rugatus* (Ibr.) S. W. & B.
295. *E. zonalis* (Loose) Knox, comb. nov.

Spores of CALAMOSPORA S. W. & B. (figs. 296–301).

FIG.
296. *C. Hartungiana* Schopf
297. *C. microrugosus* (Ibr.) S. W. & B.
298. *C. mutabilis* (Loose) S. W. & B.
299. *C. obesus* (Loose) S. W. & B.
300. *C. pallidus* (Loose) S. W. & B.
301. *C. minutus* Knox, nom. nov.

Spores of RAISTRICKIA S. W. & B. (figs. 302–306).

FIG.	
302.	*R. fibratus* (Loose) S. W. & B.
303.	*R. grovensis* Schopf
304.	*R. saetosus* (Loose) S. W. & B.
305.	*R. spinososaetosus* (Loose) S. W. & B.
306.	*R. superbus* (Ibr.) S. W. & B.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3a
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14
15
16
17
18
19a
19b
20
21
22
23
24
25
26
27
28
29
30
0
50μ

Figs. 1–6. Spores of *Lycopodium Selago* group. Figs. 7–30. Spores of *L. Phlegmaria* group.

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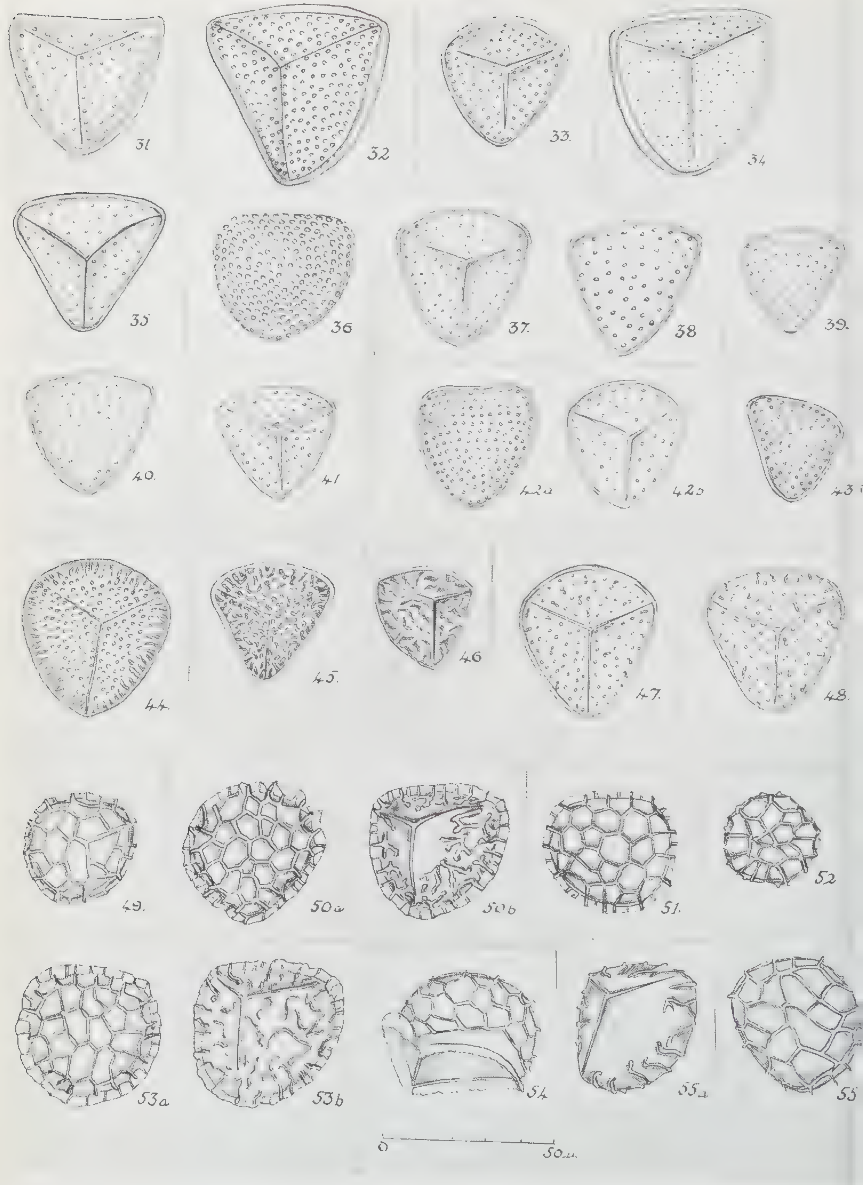
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42b
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49
50a
50b
51
52
53a
53b
54
55a
55
0
50µ

Figs. 31–43. Spores of *Lycopodium Phlegmaria* group. Figs. 44–48. Spores of *L. verticillatum* group. Figs. 49–55. Spores of *L. clavatum* group.

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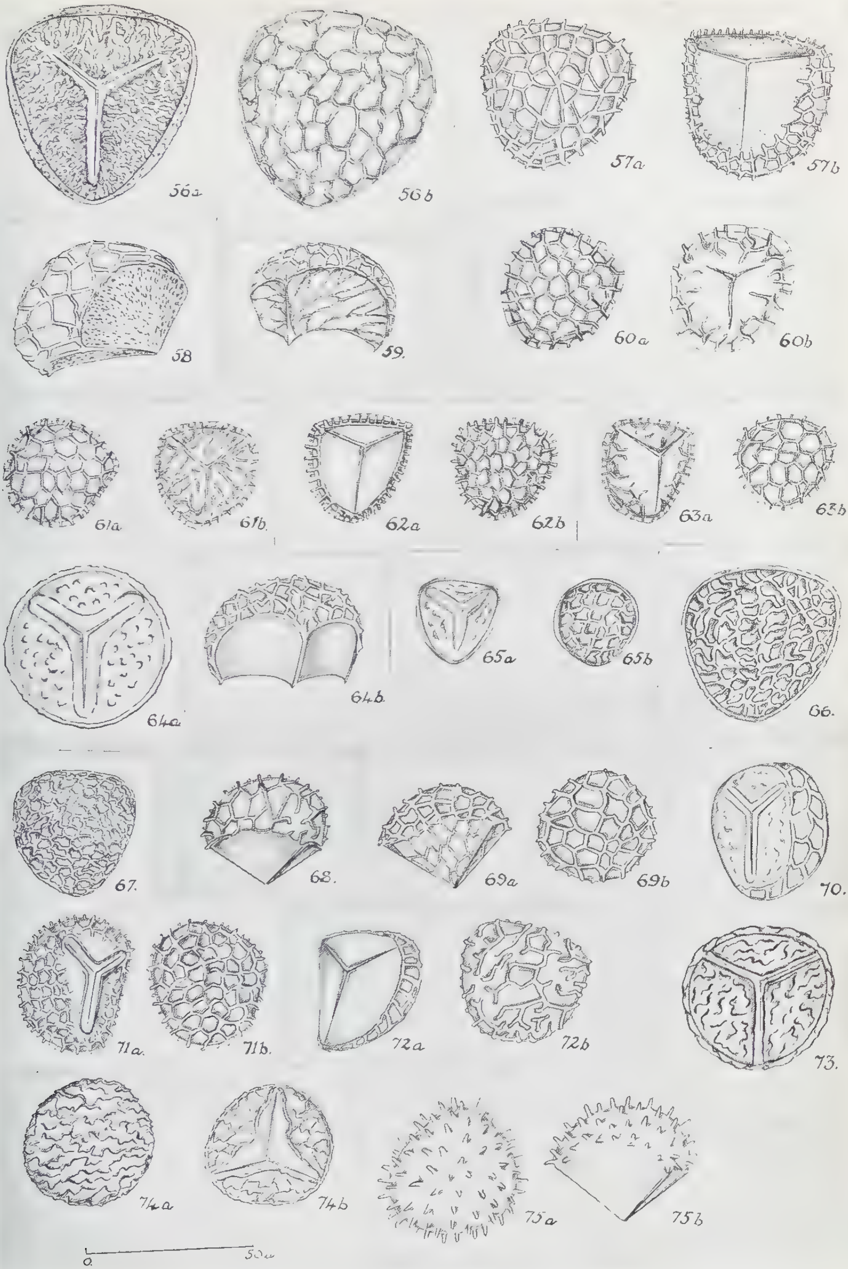
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65a
65b
66.
67.
68.
69a
69b
70.
71a.
71b.
72a
72b
73.
74a
74b
75a
75b
0
50μ

Figs. 56–74. Spores of *Lycopodium clavatum* group.
Fig. 75. *L. densum.*

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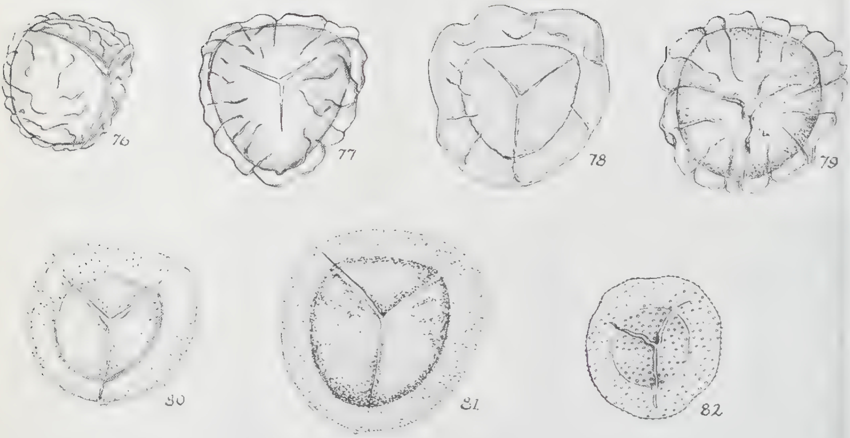
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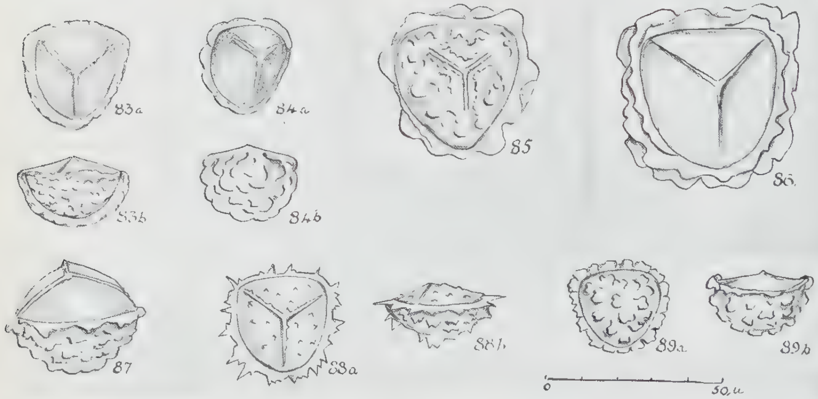
83a
84a
85
86
83b
84b
87
88a
88b
89a
89b
0
50 μ

Figs. 76–82. Spores of *Selaginella sibirica* group. Figs. 83–89. Spores of *S. sanguinolent*
group

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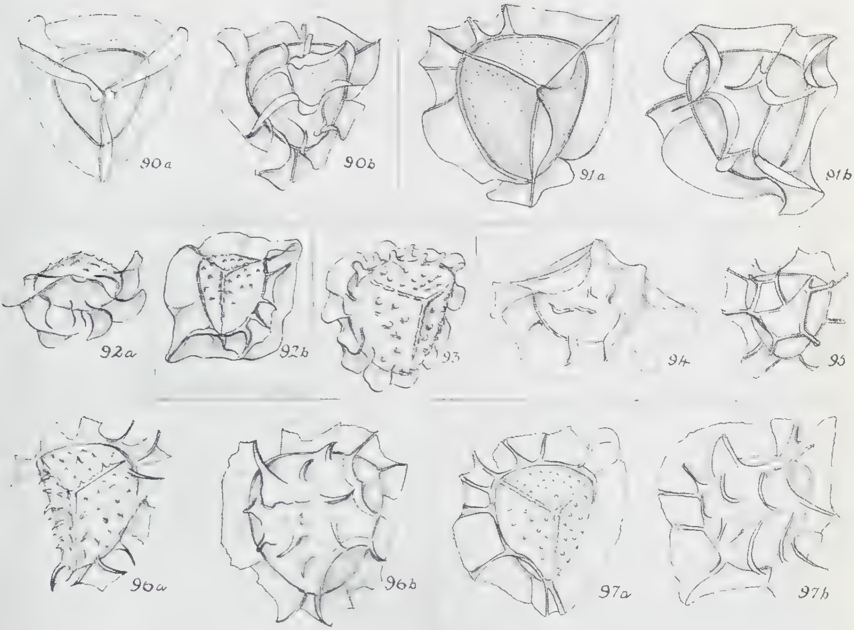
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96a
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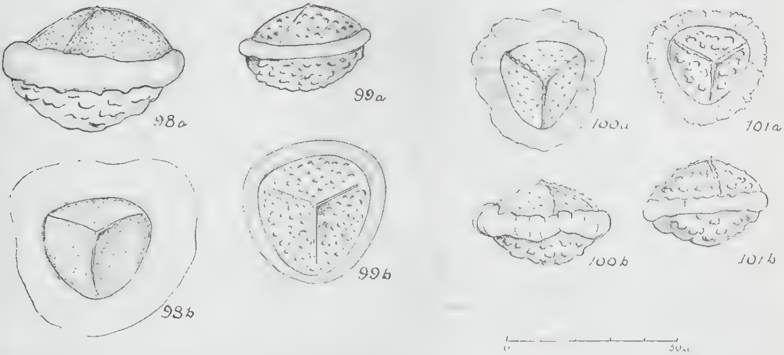
97a
97b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101b
98b
99b
0
50μ

Figs. 90–97. Spores of *Selaginella megastachys* group.

Figs. 98–101. Spores of *S. scandens* group.

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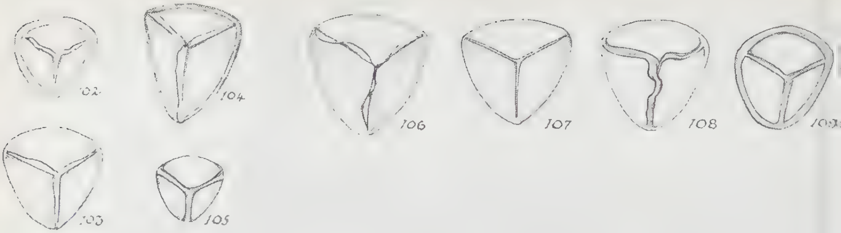
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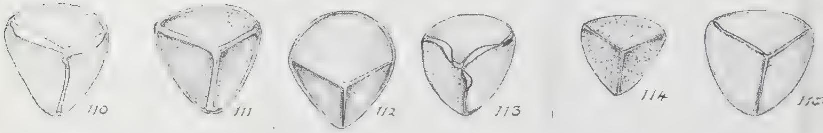
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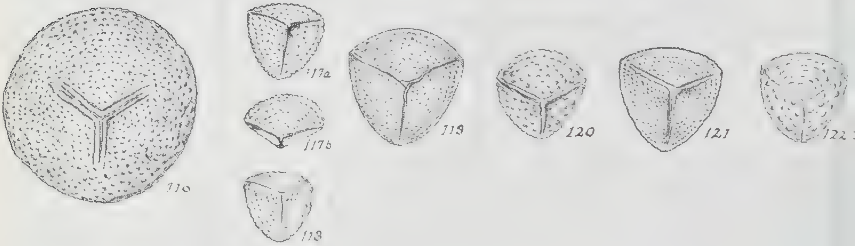
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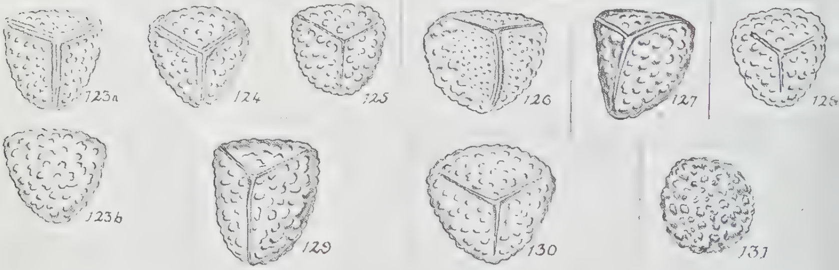
122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123b
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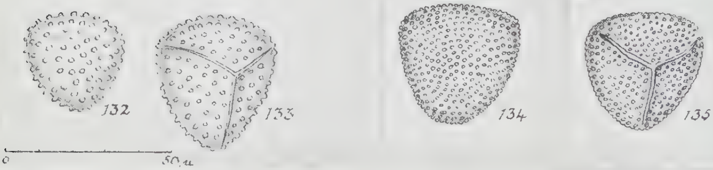
130
131


132
133
134
135
0
50μ

Figs. 102–109. Spores of *Selaginella firmula* group.
Figs. 116–122. Spores of *S. cathedrifolia* group.
Figs. 132–135. Spores of *S. leptophylla* group.

Figs. 110–115. Spores of *S. helvetica* grou
Figs. 123–131. Spores of *S. radicata* grou

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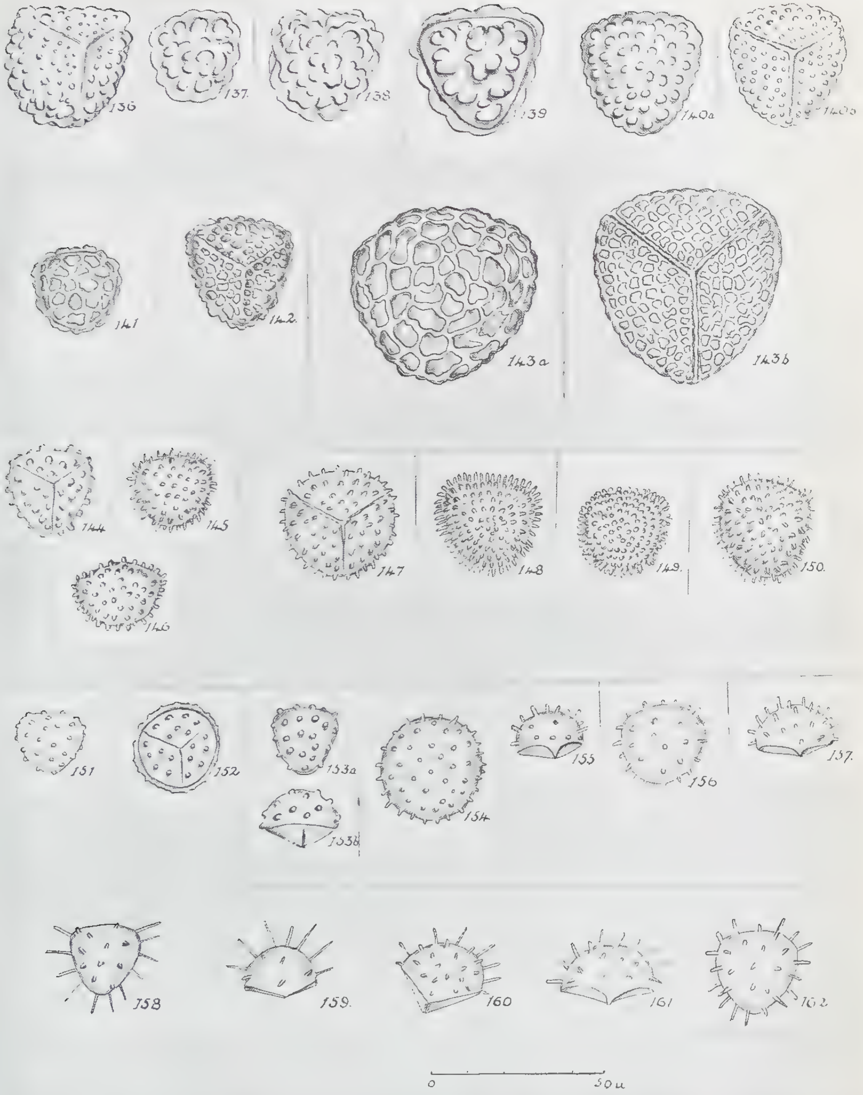
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153a
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161
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Figs. 136–140. Spores of *Selaginella vaginata* group. Figs. 141–143. Spores of *S. repanda* group. Figs. 144–150. Spores of *S. stolonifera* group. Figs. 151–157. Spores of *S. biformis* group. Figs. 158–162. Spores of *S. latifrons* group.

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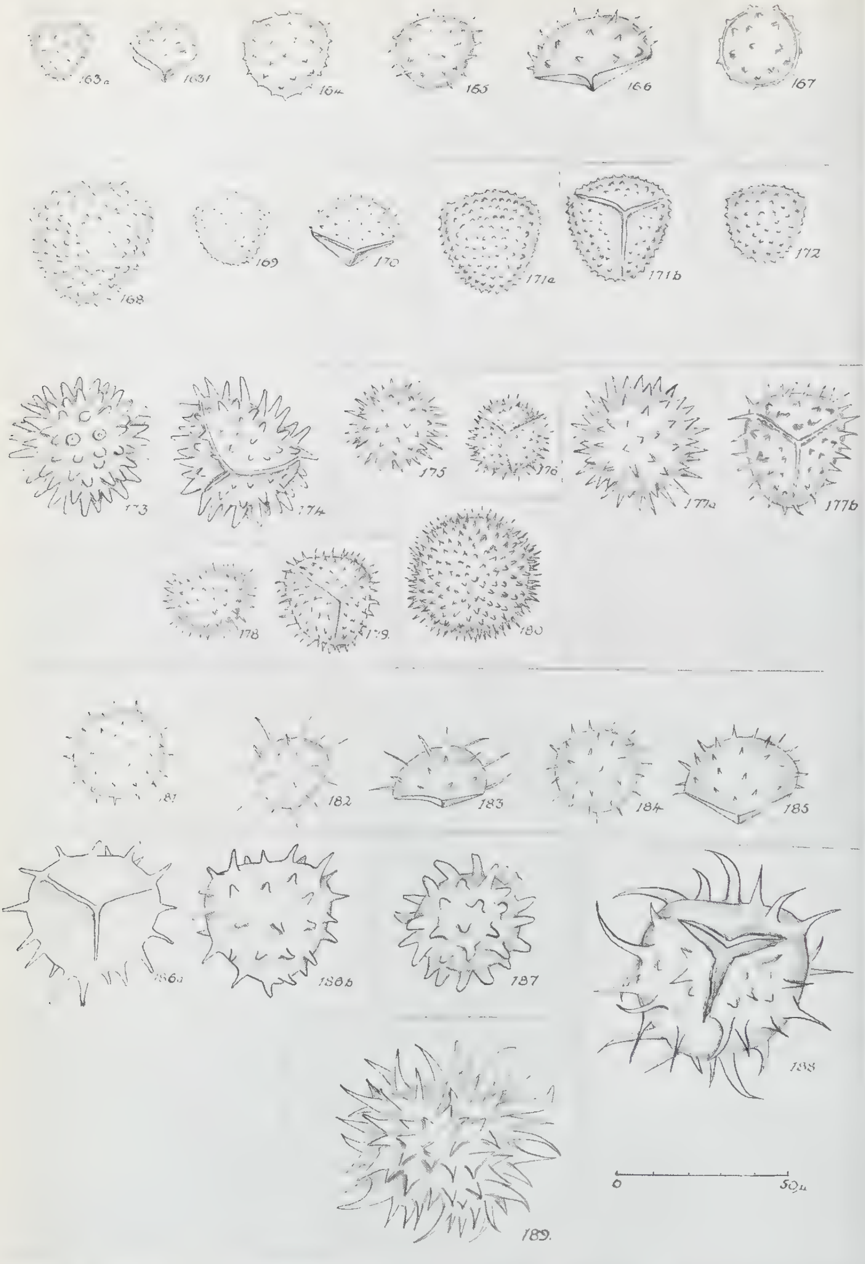
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Figs. 163-167. Spores of *Selaginella sub-arborescens* group. Figs. 168-172. Spores of *S. anceps* group. Figs. 173-180. Spores of *S. uncinata* group. Figs. 181-185. Spores of *S. magnifica* group. Figs. 186-187. Spores of *S. selaginoides* group. Figs. 188-189. Spores of *S. Kraussiana* group.

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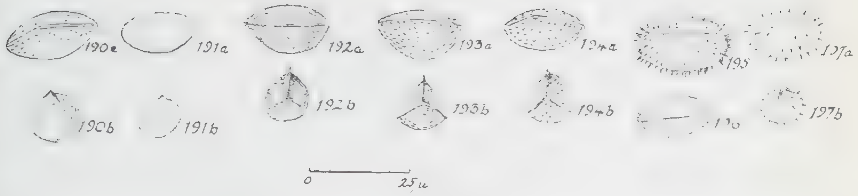
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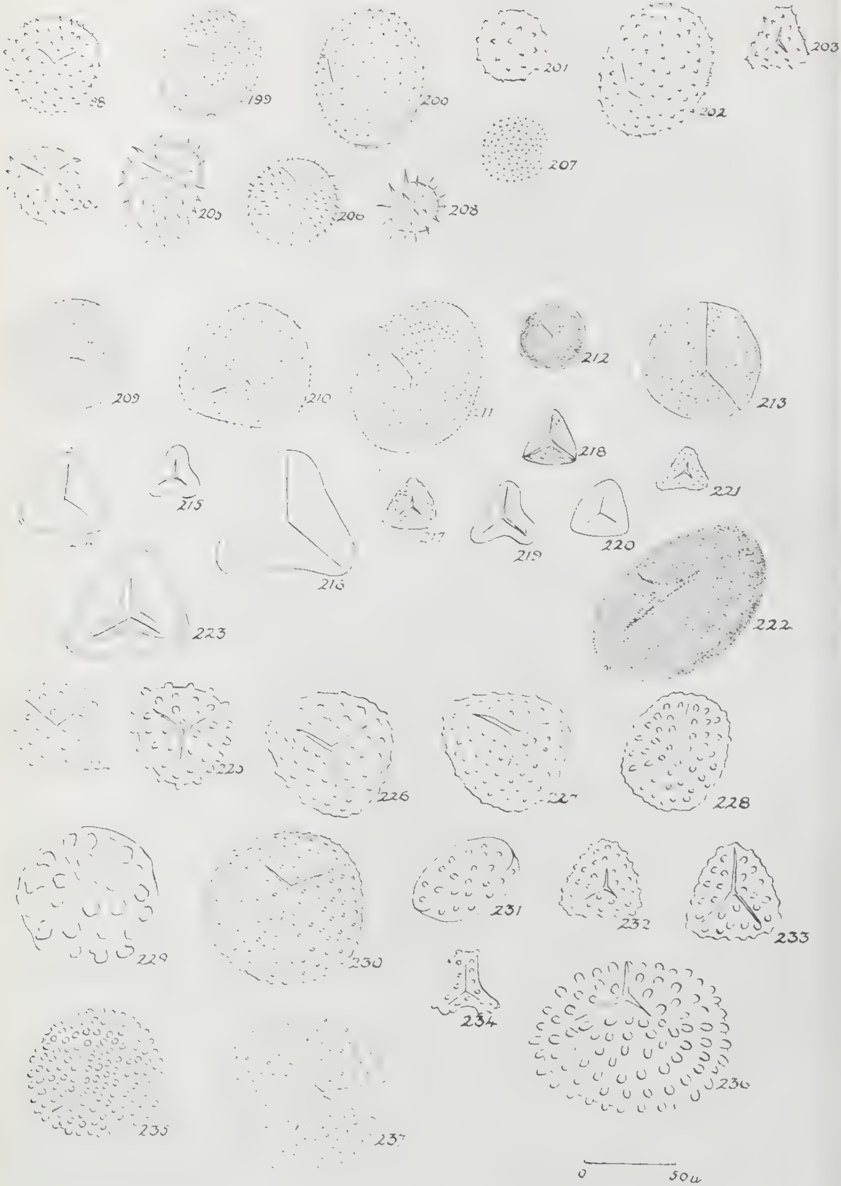
Figs. 190, 191. Spores of *Isoetes echinospora* group. Figs. 192–194. Spores of *I. adspersa* group. Figs. 195–197. Spores of *I. Hystrix* group.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Figs. 198–208. Spores of Spinoso-sporites. Figs. 209–223. Spores of Plani-sporites. Figs 224–237. Spores of Verrucoso-sporites.

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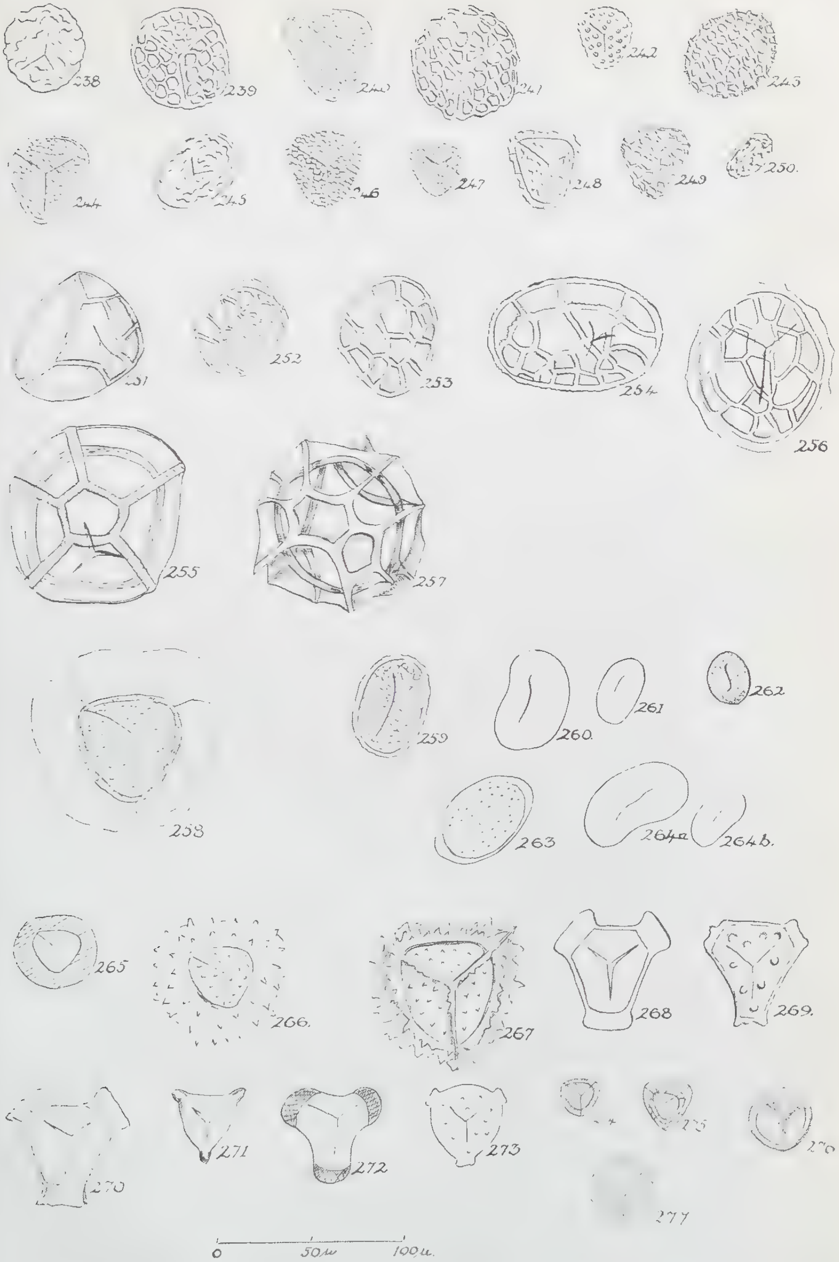
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264a
264b.
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269.
270
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272
273
274
275
276
277
0
50μ
100μ.

Figs. 238–250. Spores of Microreticulati-sporites. Figs. 251–257. Reticulati-sporites. Fig. 258. Alati-sporites. Figs. 259–264. Laevigato-sporites. Figs. 265–267. Denso-sporites. Figs. 268–273. Triquitrites. Figs. 274–277. Lycospora.

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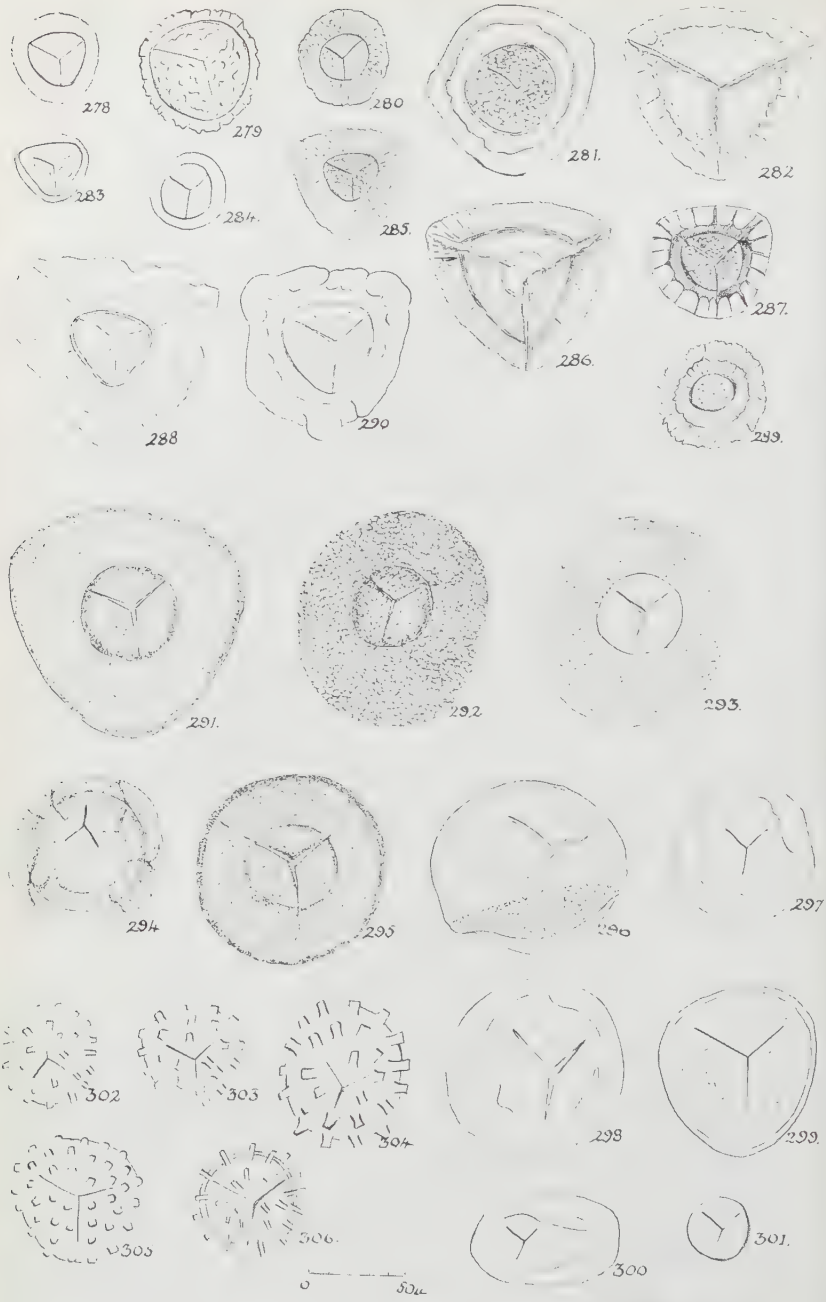
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296
297
302
303
304
298
299.
305
306.
300
301.
0
50μ

Figs. 278–290. Spores of Cirratriradites. Figs. 291–295. Endosporites. Figs. 296–301. Calamospora. Figs. 302–306. Raistrickia.

ELIZABETH M. KNOX.

TRANSACTIONS

OF THE

BOTANICAL SOCIETY OF EDINBURGH

SESSION CXIV

Report of the Meetings of the Cryptogamic Section, 1949.

By C. E. Foister.

(Read 18th May 1950.)

A spring meeting was held at the Department of Plant Pathology, West of Scotland Agricultural College, Auchincruive, by invitation of Dr. J. Grainger, on 22nd and 23rd April 1949. On the afternoon of the 22nd a tour was made of the Department of Plant Pathology, where problems encountered in advisory work and current research work were demonstrated by Dr. Grainger and Dr. Dovaston. Thereafter the work of the Department of Agriculture for Scotland's Strawberry Breeding and Disease Research unit was seen in the horticultural department, and Mr. R. D. Reid explained the purposes and results of this work. The glasshouses, used for training purposes by the College, and flower beds were visited in the company of Mr. Warwick. On Saturday, the 23rd, a successful collection of fungi, etc., was made along the borders of the river Ayr.

The sixty-first annual autumn meeting and foray was held at Dollar and district from 23rd to 25th September. Permission to foray in their estates was granted by Mr. Dickson, Factor to the late Miss Christie of Cowden Castle, and Mrs. Stuart of Arndean. Forays were held in Cowden Castle grounds, Arndean and Sheardale. Weather was quite good, but the agarics, though plentiful in number, were of relatively few kinds. Micro-fungi were not so abundant as had been found at other forays. The specimens collected were examined at the Dollar Academy, full facilities being provided by the Rector, Mr. Bell, to whom grateful thanks were recorded.

LIST OF FUNGI COLLECTED.

HYMENOMYCETES.

Amanita *citrina* (Schaeff.) Roques; *excelsa* Fr.; *rubescens* (Pers.) Fr.
Amanitopsis *fulva* (Grev.) Rea; *vaginata* (Bull.) Roze
Armillaria *mellea* (Vahl) Fr.
Bolbitius *vitellinus* (Pers.) Fr.
Boletus *appendiculatus* (Schaeff.) Fr.; *badius* Fr.; *chrysenteron* (Bull.) Fr.; *edulis* (Bull.) Fr.; *elegans* (Schum.) Fr.; *erythropus* Fr.; *scaber* (Bull.) Krombh.; *subtomentosus* (Schaeff.) Fr.; *versipellis* Fr.
Calocera *cornea* (Batsch) Fr.
Cantharellus *cibarius* Fr.
Collybia *maculata* (A. & S.) Fr.; *radicata* (Relh) Berk.
Coprinus *plicatilis* (Curt.) Fr.
Clavaria *cinerea* (Bull.) Fr.; *fumosa* (Pers.) Fr.
Clitocybe *connata* (Schum.) Fr.; *fragans* (Sow.) Fr.
Clitopilus *prunulus* (Scop.) Fr.
Craterellus *sinuosus* Fr.
Crepidotus *mollis* (Schaeff.) Fr.
Entoloma *nidorosum* Fr.; *porphyrophaeum* Fr.; *rhodopolium* Fr.; *sericeum* (Bull.) Fr.
Fistulina *hepatica* (Huds.) Fr.
Flammula *sapinea* Fr.
Fomes *annosus* Fr.; *fomentarius* (L.) Fr.
Galera *tenera* (Schaeff.) Fr.
Hebeloma *crustuliniforme* (Bull.) Fr.
Hydnum *repandum* (L.) Fr.
Hygrophorus *chlorophanus* Fr.; *coccineus* (Schaeff.) Fr.; *laetus* (Pers.) Fr.; *pratensis* (Pers.) Fr.; *psittacinus* (Schaeff.) Fr.; *virgineus* (Wulf.) Fr.
Inocybe *geophylla* (Sow.) Fr.
Laccaria *laccata* (Scop.) Cke.; *amethystina* (Vaill.) Cke.
Lactarius *blennius* Fr.; *plumbeus* Fr.; *pyrogalus* (Bull.) Fr.; *quietus* Fr.; *rufus* (Scop.) Fr.; *serifluus* (DC.) Fr.; *vellereus* Fr.
Lentinus *cochleatus* (Pers.) Fr.
Lepiota *cristata* (A. & S.) Fr.
Leptonia *sericella* (Fr.) Quél.
Marasmius *confluens* (Pers.) Karst.; *dryophilus* (Bull.) Karst.
Merulius *tremellosus* (Schrad.) Fr.
Mycena *flavo-alba* Fr.; *galericulata* (Scop.) Fr.
Nyctalis *asterophora* Fr. on *Russula nigricans.*
Panaeolus *campanulatus* (L.) Fr.
Paxillus *involutus* (Batsch) Fr.
Pholiota *flammans* Fr.; *mutabilis* (Schaeff.) Fr.; *spectabilis* Fr.; *squarrosa* (Mull.) Fr.
Pistillaria *quisquiliaris* Fr.
Pluteus *cervinus* (Schaeff.) Fr.
Polyporus *adustus* (Wild.) Fr.; *betulinus* (Bull.) Fr.; *caesius* (Schrad.) Fr.; *giganteus* (Pers.) Fr.; *nummularis* (Bull.) Quél.; *squamosus* (Huds.) Fr.
Polystictus *versicolor* (L.) Fr.
Psalliota *arvensis* (Schaeff.) Fr.; *silvatica* (Schaeff.) Fr.

Russula *atro-purpurea* Krombh.; *cyanoxantha* (Schaeff.) Fr.; *emetica* (Schaeff.) Fr.; *farinipes* Romell; *fellea* Fr.; *foetens* Fr.; *fragilis* Fr.; *gracillima* J. Schaeffer; *nigricans* Fr.; *ochroleuca* Fr.; *puellaris* Fr.; *sororia* Fr.; *vesca* Fr.

Stropharia *semi-globata* (Batsch) Fr.

Tricholoma *columbetta* Fr.; *imbricatum* Fr.; *loricatum* Fr.; *terreum* Fr.

Tubaria *furfuracea* (Pers.) Gillet

GASTEROMYCETES.

Scleroderma *aurantium* Pers.

UREDINALES.

Coleosporium *senecionis* Fr. on *Tussilago farfara* L.

Melampsoridium *betulinum* Kleb. on *Betula* sp.

Puccinia *lemonnieriana* Maire on *Cirsium palustre* (L.) Scop.; *lychnidearum* Link on *Melandrium dioicum* (L.) Goss. & Germ.

Pucciniastrum *epilobii* Otth. on *Chamaenerion angustifolium* (L.) Scop.

USTILAGINALES.

Urocystis *anemones* (Pers.) Wint. on *Ranunculus repens* L.

Ustilago *violacea* (Pers.) Rous. on *Melandrium dioicum* Coss. & Germ.

ASCOMYCETES.

Nectria *cinnabarina* (Tode) Fr.

Peziza *aurantia* Pers.

Phyllactinia *corylea* (Pers.) Karst. on *Acer pseudo-platanus* L.

Xylaria *hypoxylon* (L. ex Fr.) Grev.

FUNGI IMPERFECTI.

Pycnostysanus *azaleae* (Peck) Mason on Rhododendron buds.

MYXOMYCETES.

Mucilago *spongiosa* Morgan

THE PLANKTON OF SOME LAKES AND POOLS IN THE NEIGHBOURHOOD OF THE MOOR OF RANNOCH. By E. M. LIND, Ph.D., D.Sc.

(Read by title, 18th May 1950.)

In July 1946 a party of botanists visited Rannoch in order to study the ecology of the moor and surrounding hills. At the same time a number of plankton samples were taken from lakes and bog pools and are described in this paper. The collections were examined the same day, and some, especially those from shallow stony lochans where it was difficult to tow the net, proved to be so poor in species of phytoplankton that they were discarded. Of the eight which were retained, two were from Loch Laidon and Loch Ossian, lakes of considerable size, while the remaining six came from much smaller lochans or peaty pools.

DESCRIPTION OF LOCHS.

LOCH LAIDON.

A large loch about 6 miles long and ½ mile broad and reaching 125 feet in depth. It is fed by numerous streams flowing from the steep slopes of the hills to the north and from gently sloping bog to the south. The river entering at the west end drains a large boggy area in which lies Loch Ba, while at the other end the River Gour leaves the loch to flow down the valley to Loch Rannoch. The vegetation of the bays includes *Litorella*, *Isoetes*, *Sparganium affine*, *Myriophyllum spicatum*, *Potomageton natans* and *Juncus fluitans.*

LOCH OSSIAN.

A pleasant loch with a rocky shore about 3½ miles long and ½ mile broad, lying between the steep, wooded slopes of Carn Dearg and the bare and more gentle slopes of Bein na Lap opposite. It reaches a depth of about 100 feet and is fed by streams from the steep hillsides as well as from the bog at the west end. At the other end stands Corrour Lodge with its wooded estate. The lake is popular with anglers.

Lochan Sron Smoer.

A large stony lochan about 20 feet deep lying between the steep, birch-covered slope of Sron Smoer and a gently sloping area of blanket bog. *Litorella* and *Lobelia* are frequent on the shallow shore. This lake also is frequented by anglers.

Lochan a Mhaidseir.

A large shallow tarn with a rocky bottom surrounded by peat and fed by a stream. It is situated at about 1050 feet on the moor to the south of Loch Laidon. In the bays grow *Phragmites* and *Carex rostrata*, while *Lobelia*, *Ranunculus flammula*, *Juncus articulatus*, *Menyanthes* were noted round the margin.

Lochan Coire na Meinne.

Situated south of Loch Laidon, near the fence which marks the county boundary, at an altitude of 1131 feet and surrounded by wet *Scirpus* bog with much *Sphagnum* and *Molinia*. A large lochan with many inlets and bays filled with *Carex rostrata*, and *Lobelia* and *Juncus fluitans* frequent round the shallow margin. The plankton of this lochan was very rich in species.

Lochan Ruighe nan Sligean.

One of the many smaller lochans lying south of Loch Laidon high up in the *Scirpus-Molinia* bog. It is smaller than Coire na Meinne and has fewer bays but the same phanerogamic vegetation. It is not nearly as rich in species.

Lochan B.

A small circular pool near the south-west end of Loch Laidon and situated in a growing bog where the *Sphagnum* cover was complete. The pool was several feet deep and had no phanerogamic vegetation.

Lochan 4.

Another deep peaty pool surrounded by *Scirpus* bog with *Eriophorum angustifolium* and *Calluna*. No vegetation but much filamentous algae.

It will be seen that all these bodies of water, whether large or small, receive some drainage from peat bog. Some, however, derive part of their drainage from mountain streams. Loch Ossian, for instance, lies mainly between two hills from whose slopes streams enter the lakes, while Sron Smoer and Laidon have steep hill-slopes on one side and extensive bog or gentle slopes with blanket bog on the other.

In a previous paper (1942) it has been shown that in certain western Irish loughs there is a clear relationship between the composition of the plankton and the nature of the drainage system. It is suggested that in the very peaty lochs the dissolved matter available to the algae is largely in the form of slightly oxidised vegetable organic matter with a high C/N ratio. In the case of the lakes fed by mountain streams the organic matter originally derived from blanket bog on the mountain slopes will have been largely oxidised by the time it reaches the lake. In addition, this water, which flows down rocky stream-beds, will contain inorganic matter of mineral origin.

In Table I the Rannoch lochs are arranged in a series beginning with the larger stream-fed lochs and ending with the peaty pools. In an intermediate position come the lochans with stony shores and mainly peat drainage.

Distribution of Plankton.

Table I shows the distribution of species which occur in more than one loch. A figure represents the percentage of this species in the total plankton, × × indicates that it was usually present in a representative count, while × denotes a rare occurrence.

It will be noted that twenty-three species occur in at least five of the eight lochs and that very few have a limited distribution. The lochs at the beginning of the series (Ossian, Laidon, Sron Smoer) are distinguished by the presence of *Asterionella*, though never in quantity, and greater numbers of *Tabellaria flocculosa* and *T. fenestrata*. They have also a preponderance of certain pelagic desmids such as *Staurastrum paradoxum*, *S. curvatum* var. *inflatum*, *S. lunatum* var. *planctonicum*, *S. gracile* var. *cyathiforme*. *S. curvatum* has a wider distribution than the var. *inflatum* and is found in abundance in the peaty pool Lochan B. *Ceratium* spp. and *Botryococcus* are relatively scarce in these lochs.

The more peaty lochs have rather fewer Chlorophyceae, more *Ceratium* and *Botryococcus* and certain desmids seem to be favoured by these peaty waters. As, however, even the large lochs have considerable peaty drainage in the whole of this boggy area, the difference is less marked than in the Irish loughs.

It is of course recognised that collections made at times of year other than July would probably show quite different relative proportions of the various plankton constituents.

Table I.

Species present in two or more Lochs.

A figure indicates percentage of total plankton.
× × indicates species present in a representative count.
× indicates a rare occurrence.

Species.	Ossian.	Sron Smoer.	Laidon.	Mhaidseir.	Coire na Meinne.	Ruighe nan Sligean.	Lochan B.	Lochan 4.
Chlorophyceae (general).								
Eudorina elegans Ehrenb.	..	..	..	..	1	1	..	..
Schizochlamys delicatula West	×	15	4	40	3·5	16·5	3	..
Gloeocystis bacillus Teiling.	..	11·5	..	..	×	×	..	..
Sphaerocystis spp.	12·5	3	23	..	1	14	7	..
Quadrigula lacustris Chodat.	×	24	..	..	× ×	×	..	..
Pediastrum Boryanum (Turp) Menegh.	..	×	×	1	×	×	..	..
Paulschulzia pseudovolvox, P. Schulz. Teiling	..	×	..	..	..	×	..	..
Xanthophyceae.								
Botryococcus Braunii Kütz.	× ×	×	2	3	1	3	3·5	1·4
Chlorophyceae (desmids).								
Gonatozygon monotaenium De Bary	..	..	×	×	× ×	4	..	..
Closterium Kützingii Bréb.	1	×	..	..	×	..	×	..
Ulna, Focke	..	×	..	..	×	..	..	..
setaceum, Ehrenb.	..	..	..	×	×	..	..	..
Pleurotaenium Ehrenbergii (Bréb.) De Bary	..	..	..	..	×	×	..	..
nodosum (Bail.) Lund.	..	..	..	×	×	..	..	..
Tetmemorus granulatus (Bréb.) Ralfs	..	..	..	×	×	×	..	..
Euastrum ansatum Ralfs	..	×	..	×	..	..	..	..
humerosum Ralfs	..	..	..	1	×	..	..	..
Micrasterias apiculata (Ehrenb.) Menegh.	..	..	×	..	2	..	×	..
conferta Lund.	..	×	..	..	×	..	..	..
denticulata Bréb.	..	×	..	..	×	..	..	..
radiata Hass.	..	×	..	..	..	×	..	..
rotata (Grev.) Ralfs	..	..	×	..	×	..	..	..
truncata (Corda) Bréb.	..	..	..	1	×	..	..	..
Sol (Ehrenb.) Kütz.	×	×	×	×	1	..	..	..

TABLE I—*continued.*

Species.	Ossian.	Sron Smoer.	Laidon.	Mhaidseir.	Coire na Meinne.	Ruighe nan Sligean.	Lochan B.	Lochan 4.
Cosmarium Botrytis Menegh	..	×	..	..	×	×	..	..
contractum Kirch.	..	×	1·5	..	4	..	..	..
depressum (Nag.) Lund.	..	×	..	×	×	×	..	..
margaritatum (Lund.) Roy & Biss.	..	..	..	×	×	..	..	..
margaritiferum Menegh.	..	..	..	×	×	..	..	..
Xanthidium antilopeum (Bréb.) Kütz.	×	2	×	..	2	×	..	..
var. *depauperatum* W. & G. S. West	..	2·5	×	1	1·5	1	×	..
armatum (Bréb).) Rabenh.	..	×	×	×	×	×	×	..
cristatum (Bréb.)	..	×	..	..	×	..	..	..
Arthrodesmus Incus (Bréb.) Hass.	..	1	5·5	..	1	×	3·5	..
Staurastrum anatinum	..	..	× ×	1·5	1	×	..	..
var. *grande* West	×	2·5	× ×	6	5	1	× ×	..
var. *pelagicum* W. & G. S. West	..	..	..	..	1	×	..	..
var. *truncatum* West	..	..	×	×	..	..	..	..
Arctiscon (Ehr.) Lund.	..	1	..	×	×	..	..	..
aversum Lund.	×	×	×	..	2	× ×	×	..
Brasiliense var. *Lundelii* West	..	×	×	×	1	×	1·5	..
Cerastes Lund.	..	..	..	..	×	×	×	..
conspicuum W. & G. S. West	×	×	×	..	1·5	..	×	..
curvatum West	..	2	2·5	1	× ×	..	28	..
var. *inflatum* nobis	..	3	3·5	..	× ×	..	..	..
dejectum Bréb.	..	..	..	..	×	×	..	..
Dickei var. *rhomboideum* W. & G. S. West	..	..	×	1·5	..	×	..	..
furcigerum Bréb.	..	..	..	..	4	×	..	..
forficulatum Lund.	..	×	×	×	..	..	..	..
gracile Ralfs	..	×	..	..	..	× ×	..	..
var. *cyathiforme* W. & G. S. West	39	×	×	1·5	..	..	..	..
longispinum (Bail.) Arch.	..	..	..	×	× ×	..	×	..
longipes (Nordst) Teiling	..	..	5	..	×	6	..	..
lunatum var. *planctonicum* West	6	..	×	..	..	..	..	..
Manfeldtii Delp.	..	..	×	1	×	..	..	..
megacanthum var. *Scoticum* W. & G. S. West	×	..	1·5	..	×	..	..	..
paradoxum Meyen.	×	6	8	..	2	1	..	..
var. *parvum* West	..	×	×	2·5	..	..	..	..
Ophiura Lund.	×	1	× ×	2	17	×	× ×	..
setigerum Cleve.	..	..	×	..	×	..	..	..
sexangulare (Buln.) Lund.	..	×	×	×	..	..	..	..

TABLE I—*continued.*

Species.	Ossian.	Sron Smoer.	Laidon.	Mhaidseir.	Coire na Meinne.	Ruighe nan Sligean.	Lochan B.	Lochan 4.
Staurastrum Tohopekaligense var. *trifurcata* West	..	..	×	..	×	..	..	..
Hyalotheca mucosa (Mert.) Ehrenb.	..	..	×	..	×	..	×	..
Sphaerozosma Aubertianum West	..	×	..	..	×	..	..	..
Cosmocladium saxonicum De Bary	..	..	..	×	×	15	..	..
pulchellum Bréb.	..	..	..	×	..	..	×	..
Gymnozyga moniliformis Ehrenb.	×	× ×	× ×	×	×	4	× ×	2·3
BACILLARIOPHYCEAE.								
Asterionella formosa Hassal.	1	×	×	..	..	..	..	..
Tabellaria flocculosa (Roth.) Kütz.	9	2·5	10	1	1	×	..	..
fenestrata (Lyngb.) Kütz.	5	× ×	19	1	..	×	×	..
Fragilaria capucina Desmazieres.	×	..	..	..	×	..		..
MYXOPHYCEAE.								
Aphanothece nidulans P. Richter	×	× ×	..	..	3	..	..	..
Coelosphaerium Nägelianum Unger	..	8·5	×	12·5	3·5	×	..	..
Merismopedia glauca (Ehrenb.) Nag.	..	×	×	1·5	..	..	×	..
CHRYSOPHYCEAE.								
Dinobryon divergens Imhof.	×	1·5	1	2·5	3	25	13	96
DINOPHYCEAE.								
Ceratium hirundinella, O.F.M.	..	..	1	..	..	2	..	× ×
cornutum (Ehrenb.) Chap. & Lachm.	..	×	..	×	12	..	×	..
curvirostre, Huitf-Kaas.	..	..	..	×	×	..	×	..
Peridinium cinctum (Müller) Ehrenb.	2	×	2	..	×	..	36	..

Species present in at least Six out of Eight Lochs.

Schizochlamys delicatula West
Sphaerocystis spp.
Botryococcus Braunii Kütz.
Staurastrum Ophiura Lund.
aversum Lund.
anatinum var. *grande* W. & G. S. West
paradoxum Meyen.
Brasiliense var. *Lundellii* West
Xanthidium armatum (Bréb.) Rabenh.
antilopeum var. *depauperatum* W. & G. S. West
× *Gymnozyga moniliformis* Ehrenb.
Tabellaria flocculosa (Roth.) Kütz.
fenestrata (Lyngb.) Kütz.
× *Dinobryon divergens* Imhof.
× In all eight.

Favoured by Soil Drainage.

Staurastrum curvatum var. *inflatum* Pearsall & Lind.
forficulatum Lund.
gracile var. *cyathiforme* W. & G. S. West
sexangulare (Buln.) Lund.
lunatum var. *planctonicum* West
megacanthum var. *scoticum* W. & G. S. West
Euastrum ansatum Ralfs
Micrasterias Sol (Ehrenb.) Kütz.
Tabellaria flocculosa (Roth.) Kütz.
fenestrata (Lyngb.) Kütz.
Asterionella formosa Hassal.

Associated with Lack of Soil Drainage.

Eudorina elegans Ehrenb.
Staurastrum furcigerum Bréb.
Cerastes Lund.
longispinum (Bail.) Arch.
dejectum Bréb.
Cosmocladium saxonicum De Bary.
pulchellum Bréb.
Tetmemorus granulatus (Bréb.) Ralfs
Pleurotaenium Ehrenbergii (Bréb.) De Bary.
Ceratium curvirostre Huitf.-Kaas.
Pleurotaenium nodosum (Bail.) Lund.

List of Additional Species.

(O. = Ossian; S.S. = Sron Smoer; L. = Laidon; M. = Mhaidseir;
C.n.M. = Coire na Meinne; R.n.S. = Ruigh nan Sligean.)

Ankistrodesmus falcatus (Corda) Ralfs	S.S.
Closterium Ralfsii var. *hybridum* Raberh.	M.
Pleurotaenium coronatum (Bréb.) Rabenh.	C.n.M.
Euastrum ventricosum Lund.	C.n.M.
inerme (Ralfs) Lund.	M.
verrucosum Ehrenb.	C.n.M.
Micrasterias Jenneri Ralfs	O.
Cosmarium reniforme (Ralfs) Arch.	L.
pyramidatum Bréb.	L.
tetraophthalmum Bréb.	C.n.M.
sphaeroideum West	M.

Xanthidium controversum var. *planctonicum* W. & G. S. West	M.
Staurastrum anatinum, four-radiate form	O.
Arachne W. & G. S. West	C.n.M.
aristiferum Ralfs	C.n.M.
Avicula Bréb.	C.n.M.
brevispinum Bréb.	O.
gladiosum Turn.	C.n.M.
natator West	C.n.M.
orbiculare Ralfs	C.n.M.
polytrichum (Perty) Rabenh.	L.
paradoxum var. *cingulum* W. & G. S. West	S.S.
Sebaldi var. *ornatum* Nordst.	C.n.M.
teliferum Ralfs	S.S.
vestitum Ralfs	C.n.M.
Spondylosium planum (Wolle) West	O.
Desmidium Aptogonum Bréb.	C.n.M.
Anabaena Lemmermanni P. Richter	R.n.S.
Chrococcus limneticus Lemm.	S.S.

NOTE ON *Staurastrum anatinum*, four-radiate form, L. Ossian.

This desmid deserves further mention. It was an important constituent of the Ossian plankton and is a striking form. It differs from the type not only in its regularly four-radiate form, but in its rather more cup-shaped semi-cells.

Carter (West, 1923) draws attention to the existence of two forms of *S. anatinum*, both recorded by West from Scottish lochs. The second form (from Loch Cuthaig) besides having more cup-shaped semi-cells and longer processes differs from the more usual form in that it lacks the marginal series of verrucae and has only one pyrenoid in each semi-cell. The Ossian desmid would appear to be a four-radiate form of the Loch Cuthaig desmid. It has the central pyrenoid and the marginal verrucae only; but its semi-cells are more cup-shaped and its processes somewhat longer.

Dimensions. Length, 41–44 μ without processes; 81–92 μ with processes. Breadth, 27–31 μ without processes; 92–119 μ with processes. Isthmus, 14–15 μ.

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CONTRIBUTIONS TO THE MARITIME ECOLOGY OF ST. CYRUS, KINCARDINESHIRE.

PART I. THE CLIFFS. By E. T. ROBERTSON, B.Sc., F.G.S.

PART II. THE SAND-DUNES. By C. H. GIMINGHAM, B.A., Ph.D.

(Read by title, 15th June 1950.)

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FOREWORD.

In a series of papers, of which the first is here presented, it is intended to give an account of the plant ecology of the maritime area in the vicinity of St. Cyrus on the Kincardineshire coast 35 miles south of Aberdeen. To a large extent the work has been carried out during three annual "field classes", conducted by the Department of Botany of the University of Aberdeen, in which members of staff and senior students have co-operated. Students have all taken part in the general survey and have also, either singly or in small groups, contributed towards the investigation of particular problems. Field-work carried out in the early part of July during the past three years has been supplemented by work in the laboratory, while weekly visits were undertaken during 1949 for the purpose of continuing routine observations. We believe that this approach to the study of plants in the field provides a valuable training which is not wholly met by ordinary class excursions, although they continue as an integral part of field instruction. From the survey of the St. Cyrus area various research problems have emerged which cannot be discussed in detail, but all the available data have been drawn upon in the preparation of the present paper. The vegetation of the cliffs is dealt with by Mrs. E. T. Robertson and sand-dune communities are discussed by Dr. C. H. Gimingham. It is a matter of regret that the students who have shared in the several investigations cannot all be mentioned by name; their assistance in the collection of data and their varied contributions to the general progress of the work are gratefully acknowledged.

J. R. Matthews.

Introduction.

The St. Cyrus area has long been of special interest to Aberdeen botanists, and numerous species occurring there have been recorded by Dickie (1860). The locality has frequently been visited by members of the University Department of Botany because of the

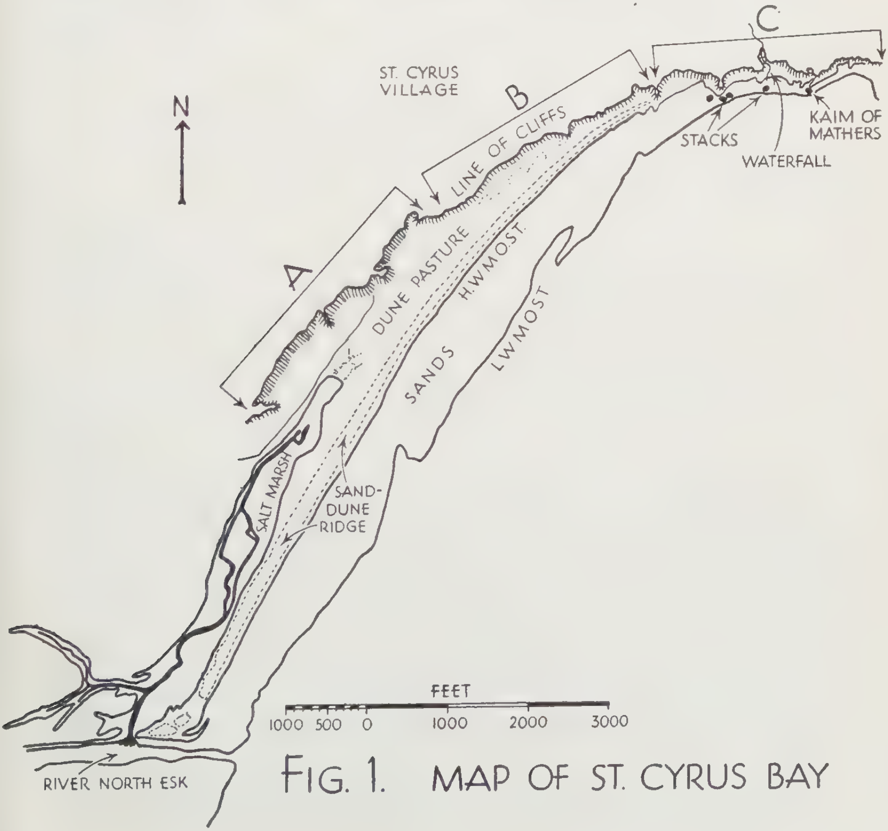
C
ST. CYRUS
VILLAGE
B
N
LINE OF CLIFFS
A
DUNE PASTURE
H.W.M.O.S.T.
L.W.M.O.S.T.
SANDS
SALT MARSH
SAND-
DUNE
RIDGE
STACKS
WATERFALL
KAIM OF
MATHERS
FEET
1000 500 0 1000 2000 3000
RIVER NORTH ESK

FIG. 1. MAP OF ST. CYRUS BAY

variety of plant communities represented and the general richness of the flora, while in recent years the region illustrated in fig. 1 has been more fully investigated from the ecological point of view. This region consists of the coastal portions of a sandy bay about 2 miles long, bounded on the west by a line of cliffs rising to 200 feet in height. A northern limit is set where these cliffs meet the sea in a series of rocky promontories, while the southern boundary is formed by the channel of the river North Esk. The cliffs run from north-east to south-west, striking away from the sea, and a flat plain, reaching about ¼ mile in width towards the southern part of the area, intervenes between the cliffs and the shore. This plain is bounded on the seaward side by a single dune ridge and its northern half is occupied by dune pasture. The remaining portion, formerly the river channel, is now salt marsh fed from the southern end where the river flows into the sea. The geological features of the area are referred to in the account which deals with the cliff vegetation, and there seems little doubt that these features, combined with favourable climatic conditions, contribute to the botanical richness of the region.

Meteorological data are not available for St. Cyrus, but the following tables * give the figures for temperature, rainfall and sunshine at Montrose (56° 42′ N., 2° 28′ W.) four miles south of St. Cyrus.

TABLE I.

MEAN TEMPERATURES IN °F., MONTROSE LINKS, 1916–20 AND 1926–35.

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Max.	43·4	44·0	46·3	49·5	54·0	59·8	63·9	63·9	59·9	53·0	47·4	43·7
Min.	33·7	33·8	35·0	37·3	41·4	46·1	50·1	50·3	46·4	41·6	37·4	35·4
Mean.	38·5	38·9	40·7	43·4	47·4	52·9	57·0	57·1	53·1	47·3	42·4	39·5

The temperature range is not great, the mean value varying only between 38·5° and 57·1°. The area is seldom subjected to rapid fluctuations or to severe extremes; the lowest average minimum being 33·7° (Jan.) and the highest average maximum 63·9° (July and August).

The total rainfall is not great and it is fairly evenly distributed throughout the year, with peaks in August and in the late autumn months. It is of interest that the total rainfall (21·79 in.) for 1949

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* Tables of means supplied by the Meteorological Office, Air Ministry. For records for 1949 we are indebted to the Burgh Surveyor, Montrose.

is notably less than the average (27·03 in.) for the period of thirty-four years from 1881 to 1915.

TABLE II.

MEAN RAINFALL IN INCHES, MONTROSE ASYLUM, 1881–1915.

Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	
1·99	1·84	2·08	1·82	2·04	1·66	2·63	2·79	1·99	2·76	2·65	2·78	27·03

ACTUAL RAINFALL IN INCHES, MONTROSE LINKS, 1949.

0·89	1·06	1·25	1·72	1·38	1·07	1·84	3·08	1·68	3·03	3·28	1·51	21·79

The figures given in Table III represent a relatively high level of insolation, reaching a maximum in June. It is believed that slightly higher figures would be obtained at St. Cyrus itself.

TABLE III.

HOURS OF SUNSHINE, MONTROSE LINKS, AVERAGE FOR 1917–35.

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	
	51	73	112	143	166	196	165	149	134	100	66	44	1399
Mean per day.	1·65	2·57	3·61	4·75	5·35	6·53	5·34	4·80	4·45	3·23	2·21	1·43	3·83
Per cent. of hours of daylight.	22	27	31	33	33	37	31	32	35	31	27	21	31

SUNSHINE DATA FOR 1949.

Mean per day.	1·9	3·8	3·7	5·3	6·8	7·6	5·1	4·3	4·2	3·5	1·9	1·8	4·2

The prevailing winds are from the south-west, but when monthly records are analysed it is apparent that the influence of south-west winds is greatest from October to May. Throughout the summer there is more variation in wind direction and a greater contribution from the north and east. Winds of high velocity are rare. During 1949, according to records taken twice daily, no month shows more than four entries for wind with a force greater than 8 (Beaufort Scale).

The topographical features of the area and the meteorological conditions together present a favourable environment with few extremes. This is reflected in the relative richness of the flora, which includes a considerable representation of southern species. The influence of the sea is felt in the maintenance of a fairly steady temperature, resulting in relatively mild winters and cool summers. Rain in August prevents drying out, in spite of a rather low total rainfall; there is abundant sunshine and few strong winds. In addition, the north-east to south-west orientation of the cliffs reduces the impact of the prevailing south-west winds, and anemometer readings suggest that upward currents will lift even inshore winds, so that their velocity is reduced over the plain and the cliff-face.

Part I. The Cliffs.

Published work on the ecology of cliff vegetation in the British Isles is relatively scanty, but various authors, including Crampton (1911), Petch (1933), Praeger (1934), Vevers (1936), Tansley (1939), Hepburn (1943), and Asprey (1947), have given some account of the flora of particular cliffs in different parts of the country. No general account is yet possible, and the present contribution is essentially a study of the flora and vegetation of the cliffs at St. Cyrus based upon data obtained from field surveys and the examination of certain habitat factors, together with reference to results of autecological and experimental studies on particular species, in so far as these have a bearing on the general problems of cliff vegetation in this area. The communities described are not all typically maritime, since along part of their length the cliffs lie some distance from the shore (fig. 1).

Geology.

The cliffs, which vary in height from 50 to 200 feet, are built of basic lava flows of Devonian age, varying somewhat in composition laterally. Towards the south they are composed of a series of flows of grey-blue basalt of varying thickness. The vesicular tops of these flows weather rapidly to form crumbly ledges alternating with bluffs of harder rock. Where numerous small faults occur, brecciation gives more easily weathered patches, and in some cases damp or dry channels occupy the lines of larger faults. The lower part of the basalt cliff towards the south (region A in fig. 1) is covered by a talus slope at about 45°, consisting of boulders and fragments of basalt from the cliff above. Passing northwards, the amount of blown sand increases greatly so as to cover completely the basal scree slopes and in some places the entire height of the cliff (region B in fig. 1).

North of this sand-covered region the composition of the lava alters to a mixture of red and green andesites, which offer more resistance to the effects of weathering and are not so clearly built up into flows. Portions of contemporaneous sandstones and conglomerates are included in the igneous rock. Partly as a consequence of this lateral change in composition, the northern part of the cliffs has not weathered so far back from the sea and the shore line is uneven, forming a series of bays and promontories with numerous isolated stacks. Thus, in the northern part of the area (region C in fig. 1) the cliffs are, at least in part, true sea cliffs, exposed to wind carrying a large amount of salt from the sea. Comparatively little blown sand reaches this northernmost part of the cliffs.

Soils.

The soil on the cliffs is generally sparse, made up of an admixture of rock debris and blown sand in varying proportions, with a low content of organic matter.

On the southern part of the cliffs soil is confined to the ledges, the tops of the lava flows and the basal scree slopes; farther north it is deeper and covers the cliffs more generally, with the greatest amount of sand in the middle region.

In July 1949 soil samples were taken from each of the three different cliff regions, at intervals from base to top of the cliff. Soil acidity, moisture content and chloride content were determined.* In addition, throughout the year 1949 measurements of these characters were carried out each week on soils from a number of fixed stations. Only the general results of these observations are used here to give an indication of the varying soil conditions.

On the entire cliff, pH values of the soils ranged, in July 1949, from 4·7 to 7·5, the more sandy soils tending to be more nearly neutral in reaction. On the southern cliffs there is a general trend from acid soil near the top to neutral at the base where the cliffs meet the dune pasture. Exceptionally basic patches (up to pH 8·2) may indicate the presence of calcite veins.

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* The methods used were as follows:—
- (*a*) pH: electrometric (glass electrode).
- (*b*) moisture: drying to constant weight at 100° C.
- (*c*) chloride: titration of filtered extract with dilute silver nitrate solution, or by conductivity method.

Soil moisture was found to vary widely, both between the different regions of the cliff at one time and at a given station throughout the year. The lowest moisture contents were recorded, as would be expected, from the sandiest soils, where the mean total moisture of samples in early July was 8·3 per cent. of dry weight. Moisture contents in all regions sampled proved to be highest in the months of November and February, and lowest in the period May to July.

The amount of salt in the soil, expressed as g. NaCl per 100 g. air-dry soil, is least in the southern parts of the cliff, which are farthest from the sea, and greatest in the northern sea cliffs. In July the mean value for the southern cliffs was 0·021 per cent., and for the northern cliffs 0·163 per cent., with an intermediate value for the intervening region. These figures are mean values calculated from all samples, ignoring height above sea-level, but a slight decrease in salt content was found in samples taken in series from base to top of the cliff. This change is most marked in the region nearest to the sea, where the salt content in one place was found to fall from 0·296 per cent. at the base to 0·111 per cent. at the top.

Salt content is also found to fluctuate considerably throughout a year, the highest amounts occurring at dry periods following storms. When the amount of salt in the soil is considered in relation to soil water—*i.e.* expressed as per cent. NaCl in soil water—the values are found to be very variable, with some extremely high figures during periods of low rainfall. Throughout 1949 the weekly samples showed at one locality in the northernmost sea cliffs (region C) a minimum value of 0·17 per cent. in August (a month of high rainfall) and a maximum of 51·6 per cent. in June (the driest summer month). In the sandy region (B) the comparable figures are 0·13 per cent. in December and 35·5 per cent. in September. In the latter case, in which much of the soil surface is exposed directly to the atmosphere, these extremes probably relate more to evaporation than to rainfall, since in December a moderate rainfall is combined with the lowest sunshine average of the year, while September has a high sunshine record.

Thus it appears that soil moisture and salt content may be factors of importance in influencing the types of vegetation found in various parts of the cliffs. The soils are in general infertile, due to drought, lack of fine particles and in some areas high salinity. The most fertile soils are at the tops of the scree slopes and in the damper gullys, where there are seepage areas or drainage channels.

The Vegetation of the Cliffs.

An appendix contains a list of all species so far recorded. The number of angiosperms and pteridophytes is 179, but the records of cliff bryophytes and lichens are still very incomplete. The number of ferns is surprisingly low; for example, *Asplenium marinum*, found elsewhere on the north-east coast, is not recorded. The list of angiosperms includes some species typical of sea-cliff vegetation such as *Plantago maritima*, *P. coronopus*, *Armeria maritima*, *Koeleria gracilis* and *Festuca ovina*, as well as species occurring commonly on sand-dunes and some others not invariably associated with maritime habitats. Amongst these is a rather characteristic group of species which, although often widespread in the south, are local or rare in the north, some of them here approaching their northern limit in Britain, *e.g. Silene nutans* and *Trifolium scabrum*. In this southern group may be mentioned also *Agropyron junceum*, *Anchusa sempervirens*, *Astragalus glycyphyllos*, *Campanula glomerata*, *Carlina vulgaris*, *Dianthus deltoides*, *Eupatorium cannabinum*, *Filago germanica*, *Plantago coronopus*, *Trifolium striatum* and *Viola hirta*. Most of these species tend to be more frequent towards the sheltered southern end of the cliffs which is also farthest from the sea and shows a lower salt content in the soil.

The cliffs provide a number of more or less distinct habitats, which may be grouped as follows:

(1) Talus slopes on the southern cliffs (Region A, fig. 1).
    (*a*) Sand-covered talus.
    (*b*) Coarse talus not covered by sand.
    (*c*) Finer talus slopes.
(2) Rock faces.
(3) Rock ledges.
(4) Sandy slopes (Region B, fig. 1).
(5) Exposed northern sea cliffs (Region C, fig. 1).
    (*a*) Dry grassy slopes.
    (*b*) Landslide areas.
    (*c*) Damp channels.
    (*d*) Waterfall.
(6) The Stacks.
(7) Summit of cliffs.
(8) Shingle.

A brief description of these several habitats may now be given.

(1) *Talus slopes on the southern cliffs* (fig. 2).

(a) *Sand-covered talus.*—Where the scree slopes have spilled on to the dune pasture at the base of the southern part of the cliffs, they have been covered by a thick deposit of blown sand; this has resulted in a hummocky stretch of ground rising gently towards the cliff. Bracken is dominant in this area and on all the screes, and in recent years has been advancing rapidly towards the dune pasture. Among vernal species which flower before the bracken fronds expand are *Scilla non-scripta* and *Valerianella locusta*, while *Primula vulgaris* and *P. veris* and the hybrid between them are also frequent members of this community. Other frequent plants are *Festuca ovina*, *Filago germanica*, *Galium verum*, *Holcus lanatus*, *Melandrium dioicum*, *Myosotis arvensis*, *Senecio vulgaris*, and *Veronica chamaedrys*.

(b) *Coarse talus not covered by sand.*—This area lying behind the sand-covered talus is slightly steeper, consists of large boulders more recently fallen from the cliff faces and is not covered by sand, which is present only in the deep cracks between the boulders. The ground is therefore very rough and the soil between the boulders relatively poor. Bracken is again the dominant plant, reaching a greater density than on the lower slopes. It attains a height of 6–8 feet and casts an extremely dense shade. Vernal species are less abundant, probably due to the unfavourable nature of the soil; *Primula vulgaris* occurs, but *P. veris*, *Scilla* and *Valerianella* are absent. *Urtica dioica* is abundant and in some places co-dominant with *Pteridium*, reaching the same height. In this area it is noteworthy that *Campanula glomerata* is more abundant than anywhere else in the entire region, flowering profusely in July beneath the dense shade of the bracken. Other common species are *Arctium lappa* and *Heracleum sphondylium* (in more open places), *Brachypodium sylvaticum*, *Dactylis glomerata*, *Myosotis arvensis*, *M. collina*, *Teucrium scorodonia*, *Veronica chamaedrys*, and *Viola hirta*.

(c) *Finer talus slopes.*—Towards the top of the scree slope, open patches occur more frequently, as the boulders give place to finer fragments about the size of coarse gravel, forming unstable "moving screes". Here the plant cover is very sparse; *Pteridium* and *Urtica* cease to be dominant, and colonising the temporary habitats are *Heracleum* and *Arctium*, which, though never abundant, are to be regarded as the dominant plants. Other associated species are *Brachypodium sylvaticum*, *Origanum vulgare*, *Rubus fruticosus*, and

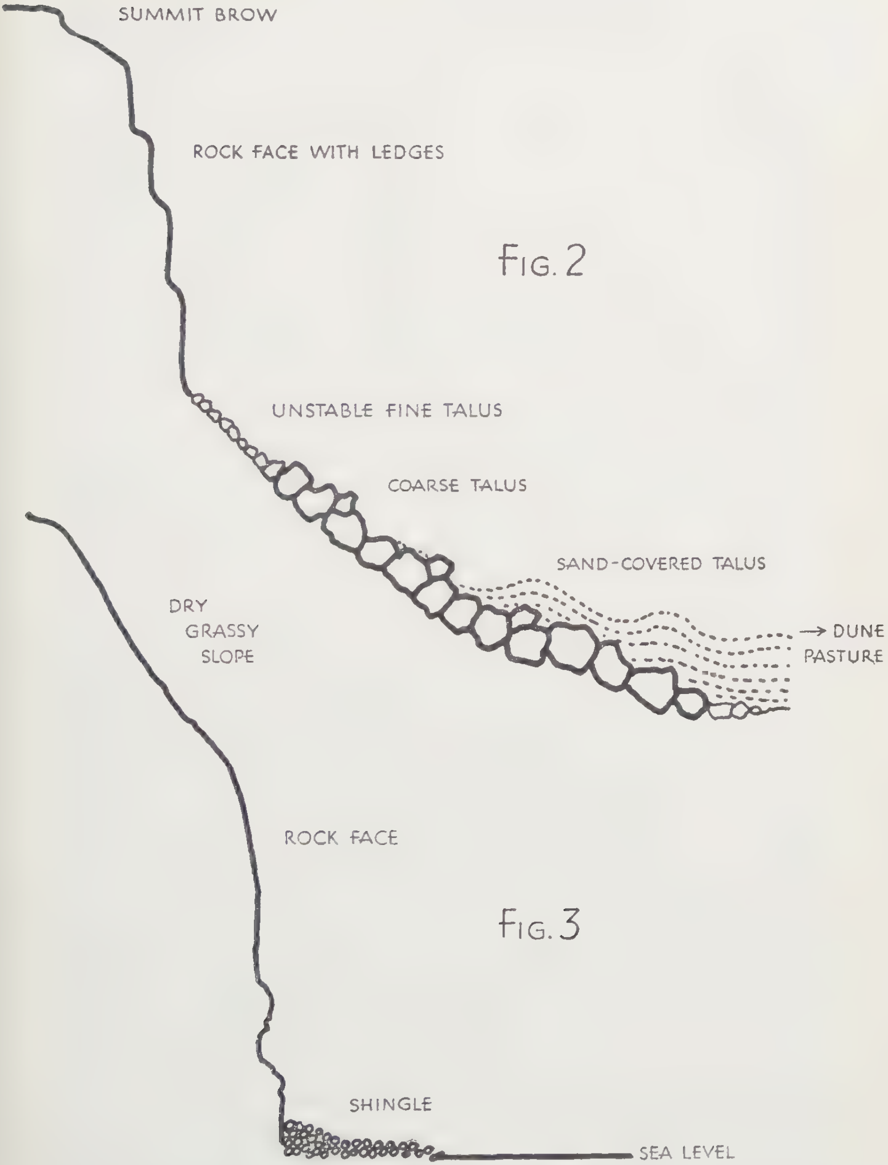
SUMMIT BROW
ROCK FACE WITH LEDGES
FIG. 2
UNSTABLE FINE TALUS
COARSE TALUS
SAND-COVERED TALUS
→ DUNE PASTURE
DRY GRASSY SLOPE
ROCK FACE
FIG. 3
SHINGLE
SEA LEVEL

FIG. 2.—Diagrammatic profile of southern end of cliffs, from region A in Fig. 1.

FIG. 3.—Profile near northern end of cliffs, from region C in Fig. 1.

Vicia sylvatica. At the very top of the scree slope *Hedera helix* covers patches of the rock face.

(2) *Rock faces.*

Where they are dry, the rock faces on the southern part of the cliff are mostly bare, with occasional lichens, small cushion-forming mosses, such as *Phascum cuspidatum* var. *piliferum* and *Bryum argenteum*, and mat-forming plagiotropic mosses such as *Camptothecium sericeum* and *Brachythecium rutabulum* colonising from cracks.

Rock faces kept wet by springs support a different and more luxuriant moss flora, including *Hypnum falcatum* and *Amblystegium filicinum.*

On the cliffs farther north the rock faces which receive a greater amount of salt spray show a slightly different assemblage of moss and lichen species, the most notable difference being the presence of *Xanthoria parietina*, which is absent from cliffs farther back from the sea.

(3) *Rock ledges.*

On the rock ledges in the south, which receive little salt spray and are more sheltered than those in the north, the following species are found: *Geranium sanguineum*, *Echium vulgare*, *Festuca ovina*, *Armeria maritima*, *Plantago coronopus*, *P. maritima*, *Silene nutans*, *Sedum album*, *S. acre*, *Astragalus danicus*, *Anthyllis vulneraria* and *Teucrium scorodonia.* It is in this habitat that some of the "southern" species occur to which reference has already been made.

In the northern more exposed sector of the cliffs with higher salt concentrations in the thin soils, the flora of rock ledges is more restricted. On the Kaim of Mathers, an extreme example, the only species are *Armeria maritima*, *Festuca ovina*, *Plantago coronopus* and *Sedum acre*, which all colonise cracks in the rock where soil has collected.

(4) *Sandy slopes.*

As already mentioned, the central area of the cliffs (Region B in fig. 1) is covered by a deep deposit of blown sand, where there occurs an assemblage of species, many of which are found also on the sand-dunes below. Certain species, however, which are not prominent members of the sand-dune community are found in considerable abundance on these sandy slopes, including *Helianthemum num-*

mularium, *Lycopsis arvensis*, *Eupatorium cannabinum* and *Brachypodium sylvaticum.* Among dune species which also occur abundantly on the slopes are *Ammophila arenaria*, *Galium verum* and *Solidago virgaurea*, which are more frequent towards the base than the top of the cliff; *Carex arenaria* and *Holcus lanatus* are more frequent at the top, while *Ononis repens*, *Origanum vulgare*, *Senecio jacobaea* and *Teucrium scorodonia* are generally distributed.

(5) *Exposed northern sea cliffs* (fig. 3).

The northernmost cliffs, nearer the sea and possessing higher salt content in the soils, support a slightly different flora from those in the south. The slopes are steeper and more uniformly covered with soil, giving way in a few places to precipitous bare rock dipping into the sea. The sand content of the soil on the slopes varies, decreasing towards the north. These slopes are of several types.

(a) *Dry grassy slopes.* These support a closed grassland community rather similar to that which occurs all along the top of the cliffs. The more abundant species are *Brachypodium sylvaticum*, *Festuca ovina*, *Koeleria gracilis* (on more exposed places), *Dactylis glomerata* and *Ulex europaeus.*

(b) *Landslide areas.* In one or two places the steepness of the slope has resulted in a landslide which has cleared the vegetation completely. Some of the bare areas so formed have been colonised by *Hyoscyamus niger.* We are indebted to Mr. A. MacGregor, Aberdeen, for the information that about fifteen years prior to our observations this species, although present, was very scarce in the area. In 1947 it was not abundant, but the following year it had colonised a portion of the cliff from top to bottom and was extending its area. Since then parts of these slopes have become stabilised with the entry of such species as *Arctium lappa*, *Cirsium arvense* and various grasses, and given a sufficient depth of soil, the final phase may be *Pteridietum.* Further landslides, however, have again opened parts of the area, with the result that the population of *Hyoscyamus* is maintaining itself.

(c) *Damp channels.* These receive drainage water from above and support a more luxuriant flora including *Hypericum quadrangulum*, *Filipendula ulmaria*, *Urtica dioica*, *Orchis mascula*, *Juncus effusus*, and *Equisetum arvense.*

(d) *Waterfall.* In particularly damp conditions, exposed to the spray of a waterfall, *Epilobium hirsutum* occurs in the precise place described by Dickie in 1860—the only locality for this plant in the area. Among other species of this habitat are: *Mimulus guttatus*, *Nasturtium officinale*, *Cochlearia officinalis*, *Rumex obtusifolius*, *R. crispus*, *Epilobium palustre*, *Phalaris arundinacea* and *Festuca arundinacea*, together with abundant bryophytes including *Conocephalum conicum*, *Eurhynchium rusciforme* var. *atlanticum* and *Brachythecium rivulare*.

(6) *The Stacks.*

The stacks consist of isolated outcrops of red and green andesites and vary greatly in size, and in distance from the sea and the main cliff. In all, 68 species have been recorded from the stacks, of which 42 are flowering plants, 13 lichens and 13 bryophytes.* Almost all of the flowering plants are common to the cliffs and the stacks, with the notable exception of *Artemisia maritima*, which has been found on one stack only and has not been observed elsewhere in the entire area. It is typically a plant of salt marshes, but does not occur on the salt marsh at St. Cyrus; it is rare in Scotland but is recorded southwards from v.c. 93 (North Aberdeen) on the east coast and v.c. 75 (Ayr) on the west. *Hyoscyamus niger*, *Campanula glomerata*, *Brachypodium sylvaticum* and other species are common to stacks and cliffs.

The bryophytes include *Metzgeria furcata*, growing on the rock of the landward side or amongst grasses in sheltered places; *Madotheca thuja* and *Grimmia maritima* are not uncommon, both mainly atlantic species, the latter typically found on rocks exposed to sea spray.

Although most of the stacks in the area were examined, one was studied in some detail. This stack is about 30 feet in height, on a base 50 × 20 feet, with its long axis aligned in a north-south direction, so that the stack presents its southern end to the sea. The eastern side is almost perpendicular, while the others descend in drops and ledges. At high tide the stack is almost surrounded by the sea, and thus the seaward end and the western side come under the direct influence of sea splash and spray.

A spray-collecting apparatus was placed among plants of *Armeria* and *Koeleria* about 18 feet above H.W.M. on the seaward side of the stack, the collecting surface being inclined at the same angle as the rock (*i.e.* about 45°). Records were made throughout a year of the volume of water falling on the exposed surface over periods of seven days, and of the amount of salt in solution. The water collected included rain as well as spray, and the volume varied greatly according to rainfall, but it was found that during periods of high winds as much as 100 c.c. per 100 sq. cm. could be collected in a week of very low rainfall. Such periods coincided markedly with those in which the greatest amounts of salt were recorded, reaching 0·05 g. NaCl per 100 sq. cm. per week. The arrival of appreciable quantities of salt appears to be restricted mainly to the months of December to May, and in the remainder of the year amounts greater than 0·006 g. per 100 sq. cm. per week were very exceptional. It may be tentatively suggested that in this situation a quantity approaching 0·5 g. of salt might be deposited on an area of 100 sq. cm. during the year.

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* In the Appendix, species occurring on the stacks are marked S.

Soil samples collected and analysed weekly from the immediate vicinity of the spray-collecting apparatus showed over a year a mean value of 0·08 g. NaCl per 100 g. air-dry soil, with largest amounts in the period April to July (maximum 0·84 per cent.) and a minimum value of 0·02 per cent. in December. This can be interpreted, in the light of the data concerning the arrival of salt in spray, as a result of the amount of salt in the soil increasing during the first four or five months of the year, remaining high during the dry months of early summer (May to July), and then gradually decreasing in the latter part of the year when a low level of arrival in spray is combined with high rainfall.

Measurement of salt content in soils at different heights on the stack have not been made, but it seems reasonable to expect this to vary with height and exposure. A clear zonation of the vegetation can be seen on this stack, which is most probably correlated with variations in salt content of the soil.

The basal 2 feet of the rock surface on the seaward side is clothed with *Pelvetia canaliculata*; above this to H.W.M. the rock is mostly bare, while lichens appear just above H.W.M. Of these the most important is *Xanthoria parietina*, covering about 25 per cent. of the rock surface for about 16 feet, with other crustaceous lichens such as *Lecanora atra*, *Callopisma citrinum* and *Diploicia canescens* rather infrequent but increasing upwards. At about 16 feet above H.W.M. flowering plants appear, first *Armeria* and *Koeleria*, and a few feet higher *Cerastium tetrandrum* and *Sedum acre*. On the higher ledges and on the top of the stack these plants appear again in a grass community consisting largely of *Festuca ovina*, *Koeleria gracilis* and *Brachypodium sylvaticum* with *Silene maritima*, *Thymus serpyllum* and *Campanula glomerata*. It is in this society that *Madotheca thuja* and *Metzgeria furcata* occur, as well as *Peltigera canina*. The amount of *Xanthoria* decreases with the decrease of bare rock until it is absent from the closed plant communities on top and on the ledges.

A certain amount of evidence for the nature of the plant succession is available from the examination of this and other stacks. It is suggested that the sequence starting with bare rock colonised by lichens (*Xanthoria* in the spray zone, with *Lecanora atra* and others higher up) and small cushion-forming mosses such as *Zygodon stirtoni* and *Grimmia maritima*, passes through a stage in which *Camptothecium sericeum* and *Hypnum cupressiforme* colonise, especially on more or less horizontal rock ledges, followed by *Sedum acre*, and later, when some soil has collected, by *Festuca ovina*. Rock crevices are also colonised by *Sedum acre* and *Plantago coronopus*, giving place to grasses, particularly *Festuca ovina* and *Koeleria gracilis*. On the ledges and tops where more soil can collect, following the sequence already described, a further change can be recognised, involving *Thymus*, *Sedum*, grasses, lichens (including *Peltigera canina* and *Cladonia* spp., some of which are epiphytic on *Sedum*), and liverworts. Last of all, tall grasses, rosette plants such as *Campanula glomerata* and annuals such as *Papaver dubium* become established to form a grassland association similar to that found on the cliff-tops.

(7) *Summit of Cliffs.*

The brow of the cliffs along their whole length is occupied by a closed community of grasses, rather similar to that on drier slopes of the northern cliffs. The common grasses are *Festuca ovina*, *F. arundinacea*, *Holcus lanatus*, *Brachypodium sylvaticum*, *Dactylis glomerata* and *Arrhenatherum elatius*; and the prominent herbs are *Tragopogon pratensis*, *Plantago media*, *P. lanceolata*, *Armeria maritima*, *Campanula glomerata*, *C. rotundifolia* and *Centaurea nigra*.

(8) *Shingle.*

The shingle in bays at the north end of the cliffs is composed of water-worn pebbles derived mostly from coastal rocks farther south. On the landward side the shingle has been colonised in patches by *Potentilla anserina*, followed in many places by an open sward in which *Festuca ovina* and *Silene maritima* are the dominant plants. Other species occurring in the sward include *Armeria maritima*, *Plantago coronopus*, *Agrostis stolonifera*, *Arrhenatherum elatius*, *Cochlearea officinalis* and *Holcus lanatus*.

The habitat is a rather exacting one for plant growth, colonisation in the first place probably being determined by the ability of seeds to germinate in the spaces between the pebbles, further spread being aided by vegetative means. The community is largely restricted to plants of a xeromorphic or halophytic character.

Succession on the Cliffs.

In dealing with the stacks, reference was made to the succession of communities in the development of their vegetation. The course of succession on the cliffs as a whole is necessarily very complicated, and as yet insufficient evidence has been obtained to offer more than a few tentative suggestions.

Early colonisation on bare rock surfaces follows more or less the xeric succession described by Weaver and Clements (1929), *i.e.*, crustose lichens ⟶ foliose lichens ⟶ xerophytic mosses ⟶ herbs. At St. Cyrus the pioneer plants appear to be crustose lichens or small xeromorphic orthotropic mosses such as *Phascum cuspidatum* var. *piliferum* and *Bryum* spp., either being followed by plagiotropic "mat-forming" mosses such as *Camptothecium sericeum* and *Brachythecium* spp. Both types of moss may hold seeds of herbaceous plants and enable them to grow if the rock face remains undisturbed for a sufficiently long time for weathering and the collection of plant debris to produce a soil. On stable, more or less horizontal, rock surfaces this process occurs, but frequently the piece of rock eventually breaks off at joint faces to contribute to the talus slope below, and the succession must begin again on the new surface.

On the scree slopes, large settled boulders support some plagiotropic mosses, but further succession is prevented by the dense shade cast by bracken, which establishes itself rapidly in the sandy crevices between the boulders. The finer open screes are colonised, as already described, by *Arctium*, *Heracleum* and smaller annual and biennial plants; further succession is prevented by new falls from above initiating movement of the loose gravelly material.

Succession on cleared landslip areas has already been described, where the final stage appears to be either semi-maritime grassland or a community dominated by bracken if soil depth is sufficiently great.

Discussion.

Considering the flora of the cliffs as a whole, it appears that the moist habitats of the northern region possess a relatively rich mesophytic flora comparable to that occurring on the southern part. On the other hand, the drier habitats in the north have a restricted and more clearly halophytic flora. This can be explained by reference to the data for soil chloride and moisture, which indicate that the soils in the northern area have in general a higher salt content than those towards the southern end of the cliffs; and where moisture content is high the excess salt is leached out.

Halophytes have been defined (Chapman, 1942) as plants which can at any stage tolerate salt concentrations of 0·5 per cent. NaCl in soil water, but measurements of St. Cyrus soils show that high proportions of salt may at times be reached in areas which are not characterised by strongly halophytic vegetation, a result in agreement with views expressed by Hepburn (1943). Some experimental work on salt tolerance in *Armeria maritima* carried out at Aberdeen by Mr. R. C. Stephen gave the following results. Plants were grown in sand culture and watered with solutions containing NaCl and $MgSO_4$ (in the proportion: 100 parts by weight NaCl to 50 parts $MgSO_4.7H_2O$) at various concentrations. The experiment extended over four months. The plants watered with a 5 per cent. solution died or failed to grow, others watered with a 3 per cent. solution grew and some flowered, while maximum growth was obtained with a 1 per cent. solution. It appears that while plants of *Armeria maritima* cannot grow well in a constant salt concentration of more than 1 per cent., they can tolerate much higher concentrations for shorter periods. This is likely to occur under natural conditions when much wind-blown spray arrives in dry weather, balanced by periods of low salt content when the soil water is diluted by heavy rains, which may also leach away the salt. It is probable that this conclusion applies also to other members of the flora. It provides a close parallel to results obtained in the field by Hepburn, although the results discussed on p. 376 suggest that, on considering the whole year, a greater range of variation in concentration of salt in the soil must be envisaged than that recorded by Hepburn over a much shorter period. Much more experimental work, however, remains to be carried out along these lines before this problem can be fully elucidated.

Summary of Part I.

The distribution of species of the cliffs and stacks seems to be controlled by a number of interacting factors of which the following appear to be significant.

(a) *Shelter from winds.*—A richer flora of southern species occurs towards the south part of the cliff and in bays sheltered by promontories in the north.

(b) *Moisture content.*—This varies with the amount of wind-blown sand in the soil. Numerous species found also on the dunes occur on drier places along the whole length of the cliff and particularly in the middle region covered by sand. A less xeromorphic flora occurs in damp bays in the north.

(c) *Exposure to salt.*—This is related to force and direction of wind and to moisture content of the soil. The flora of the northern cliffs and stacks is somewhat restricted, and includes a larger proportion of halophytic species than the southern cliffs.

PART II. THE SAND-DUNES.

Sand-dunes provide an exceptionally favourable opportunity for observing the reaction of plants upon their habitat and for assessing the rôle of various individual species in a succession in which autogenic factors play a large part. This is due chiefly to the fact that in the early stages of colonisation the environment is highly exacting and the assemblage of species a simple one. The substratum is relatively uniform and not complicated in composition. Owing to the progress of colonisation, a series of stages of increasing age is established and this zonation in space makes it possible to reconstruct the succession in time and to follow the progressive modification of the habitat and the development of a complex community. It is from these points of view that the dune system at St. Cyrus has been examined.

A recent account of a sand-dune in the Outer Hebrides (Gimingham *et al.*, 1948) dealt with the vegetation of a highly calcareous dune-system (mean 58·6 per cent. of $CaCO_3$) developed under the atlantic conditions of the west coast of Scotland. The limited flora of that area (about 47 species of phanerogams) forms an interesting contrast with the rich vegetation of St. Cyrus dunes (142 species), situated only about 1° of latitude farther south, but on the east coast, where the dunes are sheltered from gales and built of a largely non-calcareous sand (mean 1·75 per cent. $CaCO_3$).

St. Cyrus dunes are composed of a single ridge running north-north-east to south-south-west, approximately $1\frac{1}{2}$ miles long, tracing the gentle arc of the bay (fig. 1). Over the greater part of its length the ridge drops very suddenly to the beach, forming a miniature scarp. It would appear that prior to about 1946 there had, for a number of years, been no building on the seaward front, and that this "scarp" is an erosion face. The prevailing winds are south-west, more or less parallel with the ridge, and during this period the only portion showing active building was the southern tip. Recently, however, a region of foreshore colonisation has appeared at the seaward edge of the dune ridge in the central part of the bay (fig. 4), in front of the scarp. This was first observed in 1948, and in 1949 appeared to have spread both northwards and southwards, while in 1950 colonisation was taking place along the greater part of the length of the ridge. In the sectors originally occupied in 1948 there has since been extension seawards from the areas first colonised which now show evidence of development into embryonic dunes, and if this process persists, the existing dune system may eventually be extended or a new parallel ridge may arise. Thus active dune-building is taking place both at the southern tip of the ridge and along its central portion. Sand movement is readily observed in high winds, and the direction is most frequently northwards. The bay, however, receives much shelter from the cliffs, and the dunes have not attained any great height, the highest point on the ridge reaching only about 50 feet.

There is one gap in the ridge and three landward-facing erosion hollows. It is probable, however, that all of these were started artificially, and wind has been responsible only for their extension. Fires are frequent on the older parts of the dunes.

Methods.

The accompanying sketch-map (fig. 4) illustrates the dune area, and the stages in succession reached in the different parts are indicated. The five stages recognised are:—

A, Foreshore colonisation.
B, Foredunes (=embryonic dunes).
C, Mobile and young fixed dunes (=yellow dunes).
D, Older fixed dunes.
E, Dune pasture.

From the areas occupied by each of these stages full species lists, accompanied by frequency estimations, were made (Table IV). Each area has also been subdivided and analysed by quadrat sampling. A metre quadrat, gridded into 36 squares, was used and the occurrence of the various species recorded in every alternate square. Quantitative data regarding the frequency, grouping and localisation of the component species have thus been obtained, the analysis being repeated in three successive years. The results cannot be presented in detail here, but provide the groundwork on which the descriptive account of the vegetation is based.

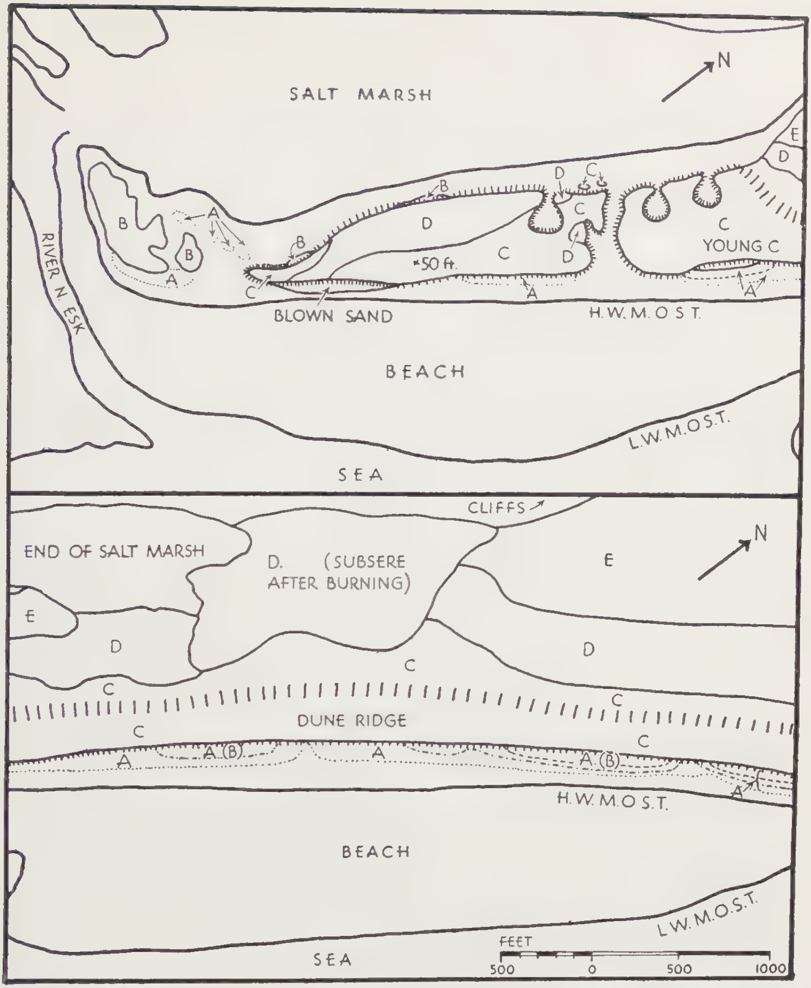
SALT MARSH
N
E
D
D
C
B
D
C
RIVER N. ESK
B
A
B
D
C
YOUNG C
B
*50 ft.
C
D
A
C
BLOWN SAND
A
A
H.W.M.O.S.T.
BEACH
L.W.M.O.S.T.
SEA
CLIFFS
END OF SALT MARSH
D. (SUBSERE AFTER BURNING)
E
N
E
D
D
C
C
C
DUNE RIDGE
C
C
A
A(B)
A
A(B)
A
H.W.M.O.S.T.
BEACH
L.W.M.O.S.T.
SEA
FEET
500
0
500
1000

Fig. 4.—Sketch-map showing stages in succession reached at various parts of St. Cyrus dunes.

A : Foreshore colonisation.
A (B) : Signs of foredune formation in areas previously at Stage A, 1950.
B : Foredunes.
C : Mobile and young fixed dunes.
D : Older fixed dunes.
E : Dune pasture.
— — — — — — — : Forward limits of Stage A, 1948.
— · — · — · — : Forward limits of Stage A, 1949.
. . . . : 1950 limits of Stage A.
/ / / / / : Gentle slope.
⌣ : Eroded slope.

Outlines approximate only. Upper section continues to the right with lower section. The sequence of the zones at the right-hand edge of the lower section continues unchanged to the northern limit of the area.

TABLE IV.

SPECIES LISTS FOR FIVE STAGES IN SUCCESSION.

	A.	B.	C.	D.	E.
Flowering Plants and Ferns					
Salsola kali	a	o	—	—	—
Agropyron junceum	f	d	o	—	—
Cakile maritima	f	o	r	—	—
Atriplex babingtonii	f	o	—	—	—
Ammophila arenaria	o	o	d	a	o
Arenaria peploides	o	o	r	—	o
Atriplex littoralis	o	—	—	—	—
Cirsium arvense	r	o	a	f	f
Elymus arenarius	r	r	o	—	—
Plantago maritima	r	r	—	—	—
Atriplex laciniata	r	—	—	—	—
Festuca rubra	—	o	a	a	a
Rumex crispus	—	o	o	r	o
Senecio jacobaea	—	r	a	a	o
Cerastium tetrandrum	—	r	a	f	f
Holcus lanatus	—	r	o	a	a
Dactylis glomerata	—	r	o	f	a
Myosotis arvensis	—	r	o	f	f
Heracleum sphondylium	—	r	o	f	o
Ranunculus repens	—	r	o	o	o
Sonchus asper	—	r	o	o	o
Plantago lanceolata	—	r	r	f	a
Rumex acetosella	—	r	r	r	o
Cirsium vulgare (lanceolatum)	—	r	o	o	—
Sedum acre	—	r	o	—	—
Melandrium dioicum	—	r	r	o	—
Arctium lappa	—	r	r	—	—
Galium aparine	—	r	—	r	—
Potentilla anserina	—	r	—	r	—
Rumex obtusifolius	—	r	—	—	—
Tussilago farfara	—	r	—	—	—
Cerastium vulgatum	—	—	f	f	f
Hieracium sp.	—	—	f	f	r
Ononis repens	—	—	o	d	f
Solidago virgaurea	—	—	o	a	a
Arrhenatherum elatius	—	—	o	f	f
Taraxacum officinale	—	—	o	f	o
Cerastium semidecandrum	—	—	o	a	—
Arabis hirsuta	—	—	o	r	—
Symphytum officinale	—	—	o	r	—
Angelica sylvestris	—	—	o	—	o
Myosotis collina	—	—	o	—	—
Carex arenaria	—	—	r	a	a
Galium verum	—	—	r	a	a
Hieracium pilosella	—	—	r	a	a
Poa pratensis agg.	—	—	r	a	a
Trifolium repens	—	—	r	f	a
Valeriana officinalis	—	—	r	f	o
Astragalus danicus	—	—	r	o	f
Centaurea nigra	—	—	r	o	f
Ranunculus bulbosus	—	—	r	r	o
Viola tricolor agg.	—	—	r	r	o
Aira praecox	—	—	r	r	r
Thalictrum arenarium	—	—	r	a	—
Carlina vulgaris	—	—	r	f	—
Scrophularia nodosa	—	—	r	o	—
Crepis capillaris	—	—	r	—	o
Hypericum hirsutum	—	—	r	—	o
Anthyllis vulneraria	—	—	r	—	—
Chamaenerion (Epilobium) angustifolium	—	—	r	—	—
Geranium molle	—	—	r	—	—
Prunella vulgaris	—	—	r	—	—
Vicia lathyroides	—	—	r	—	—
Achillea millefolium	—	—	—	a	a
Veronica chamaedrys	—	—	—	a	a
Campanula glomerata	—	—	—	f	o
Filago minima	—	—	—	f	—
Bellis perennis	—	—	—	o	a
Euphrasia officinalis agg.	—	—	—	o	a
Koeleria gracilis	—	—	—	o	a
Lotus corniculatus	—	—	—	o	f
Hypochoeris radicata		—	—	o	o
Rhinanthus minor agg.	—	—	—	o	o
Senecio vulgaris	—	—	—	o	—
Teucrium scorodonia	—	—	—	r	a
Agrostis tenuis	—	—	—	r	f
Filipendula ulmaria	—	—	—	r	f
Rubus fruticosus agg.	—	—	—	r	o
Vicia sepium	—	—	—	r	o
Viola riviniana	—	—	—	r	o
Arenaria serpyllifolia	—	—	—	r	r
Lathyrus pratensis	—	—	—	r	r
Chrysanthemum leucanthemum	—	—	—	r	—
Melandrium album	—	—	—	r	—
Phleum arenarium	—	—	—	r	—
Rumex acetosa	—	—	—	r	—
Urtica dioica	—	—	—	r	—
Veronica arvensis	—	—	—	r	—
Anthoxanthum odoratum	—	—	—	—	a
Campanula rotundifolia	—	—	—	—	a
Thymus serpyllum agg.	—	—	—	—	a
Polygala vulgaris	—	—	—	—	a
Festuca ovina	—	—	—	—	f
Geranium sanguineum	—	—	—	—	f
Luzula campestris	—	—	—	—	f
Origanum vulgare	—	—	—	—	f
Phleum nodosum	—	—	—	—	f
Pimpinella saxifraga	—	—	—	—	f
Saxifraga granulata	—	—	—	—	f
Dianthus deltoides	—	—	—	—	o
Erodium cicutarium agg.	—	—	—	—	o
Filago germanica	—	—	—	—	o
Helianthemum nummularium	—	—	—	—	o

TABLE IV—*continued.*

	A.	B.	C.	D.	E.
Flowering Plants and Ferns—*contd.*					
Helictotrichon (Avena) pubescens	—	—	—	—	o
Primula veris	—	—	—	—	o
Primula vulgaris	—	—	—	—	o
Rosa canina agg.	—	—	—	—	o
Scilla non-scripta	—	—	—	—	o
Stellaria graminea	—	—	—	—	o
Trifolium arvense	—	—	—	—	o
Trifolium campestre	—	—	—	—	o
Ulex europaeus	—	—	—	—	o
Veronica officinalis	—	—	—	—	o
Viola hirta	—	—	—	—	o
Acer pseudo-platanus	—	—	—	—	r
(*Coeloglossum viride*)	—	—	—	—	r
Crataegus monogyna	—	—	—	—	r
Festuca arundinacea	—	—	—	—	r
Galium cruciata	—	—	—	—	r
Geranium pratense	—	—	—	—	r
Helictotrichon (Avena) pratense	—	—	—	—	r
Hypericum pulchrum	—	—	—	—	r
Leontodon autumnalis	—	—	—	—	r
Linum catharticum	—	—	—	—	r
Stellaria media	—	—	—	—	r
Tanacetum vulgare	—	—	—	—	r
Tragopogon pratensis	—	—	—	—	r
Valerianella locusta	—	—	—	—	r
Botrychium lunaria	—	—	—	—	r
Pteridium aquilinum	—	—	—		la
Bryophytes					
Bryum pendulum	—	—	a	o	—
Ceratodon purpureus	—	—	a	a	r
Tortula ruraliformis	—	—	f	a	o
Brachythecium albicans	—	—	f	a	f
Hylocomium squarrosum	—	—	o	a	a
Hylocomium splendens	—	—	r	o	f
Bryum argenteum	—	—	r	o	r
Hylocomium triquetrum	—	—	—	o	a
Hypnum cupressiforme	—	—	—	o	f
Brachythecium purum	—	—	—	r	o
Brachythecium rutabulum	—	—	—	r	o
Climacium dendroides	—	—	—	r	o
Dicranum scoparium	—	—	—	r	o
Mnium undulatum	—	—	—	r	o
Mnium cuspidatum	—	—	—	r	—
Weisia viridula	—	—	—	r	—
Eurhynchium praelongum	—	—	—	—	r
Hypnum schreberi	—	—	—	—	r
Mnium rostratum	—	—	—	—	r
Polytrichum juniperinum	—	—	—	—	r
Lophocolea bidentata	—	—	—	o	o
Cephaloziella starkii	—	—	—	r	o
Lepidozia reptans	—	—	—	—	r

The general analysis of the vegetation has been supplemented by autecological studies of the dominant species of each stage in the succession and of other important components of the communities. Considerable importance is attached to this aspect of the work, which has shed much light on the processes involved in dune formation. These are further traced by investigation of changes in the factors of the habitat, including soil, relative humidity of the atmosphere and wind, which take place with the progress of the succession.

Finally, certain special features have received attention, particularly the subsere following burning and the colonisation of the areas adjacent to the river-mouth.

The Vegetation of the Dunes.

Examples of foreshore colonisation (stage A) and embryonic dunes (stage B) occur at the southern tip of the ridge and in certain places along its seaward edge. Throughout its length, however, the ridge is occupied by vegetation belonging to stage C (early fixation), and as the ridge slopes downwards towards the land the vegetation passes uniformly into stage D (later fixation). Much of the inland area is modified by frequent fires, but in the northern part the areas of stage D pass into a well-developed dune pasture (E). This is closely grazed by numerous rabbits, which extend their activities well into the dense *Ammophiletum* of stage C. There are no dune slacks. The flowering plants, ferns and bryophytes from each stage are given in Table IV.

Foreshore Colonisation (*Stage A*).—As seen from Table IV, 11 species take part in the colonisation of the shifting sand above high-water mark, but of these only 4 occur in any abundance. Individuals of each species tend to occur in small groups, giving rise to a very open assemblage, in which as much as 81 per cent. of squares measuring $\frac{1}{36}$ sq. m. were unoccupied. Apart from a few perennials, notably *Agropyron junceum* and to a lesser extent *Ammophila arenaria* and *Elymus arenarius*, the vegetation is composed predominantly of annual species consisting primarily of *Salsola kali*, *Atriplex babingtonii* and *Cakile maritima*. The proportions in which these species occur change markedly from year to year. In 1947, when foreshore colonisation was confined to isolated areas at the southern tip of the dunes, all three species were about equally frequent, but in 1948 and 1949, when the area of colonisation extended to the main front, *Cakile maritima* almost disappeared. At first *Salsola kali* was most prominent, with *Atriplex babingtonii* a frequent associate, and in 1949 even the latter became insignificant.

The roots of *Agropyron*, *Salsola*, *Atriplex babingtonii* and *A. laciniata* all showed distinct association with the presence of buried seaweed drift. Measurements of roots of 10 plants of each of these species are given in Table V, and their rooting behaviour is found to be similar to that observed in comparable situations in Harris.

The working depth is of the same order in the four species. In the three annuals the development of lateral roots is relatively poor, although one or two per plant may reach lengths comparable with the tap root. These very constantly appear about $2\frac{1}{2}$–3 inches below the surface. The perennial grass *Agropyron* produces laterals more abundantly, often originating close to the surface. As in Harris, *Arenaria peploides*, an occasional constituent of the foreshore community, shows no regular association with seaweed drift.

Seedlings of *Salsola* and *Atriplex* appear in large numbers in April and May on the hummocks of sand which form over stranded debris.

TABLE V.

ROOT MEASUREMENTS IN INCHES.

	Depth of Longest Root.		Length of Longest Lateral.		Position of Longest Lateral below Surface.		
	Mean.	Max.	Mean.	Max.	Mean.	Min.	Max.
Salsola kali . .	8·8	14·5	8·0	13·0	2·8	1·5	4·5
Atriplex babingtonii	9·5	13·5	8·7	16·0	2·7	2·0	3·5
A. laciniata . .	6·7	8·5	3·3	4·0	2·4	2·0	3·0
Agropyron junceum	8·2	10·0	6·3	12·5	1·5	1·0	2·0

Agropyron junceum and *Ammophila arenaria* may also be found in the seedling stage at this time, and establishment from broken pieces of rhizome has also been observed in both species. The spikelet of *Agropyron* is shed as a unit and normally gives rise to a single seedling only, but seedlings of *Ammophila* are sometimes found in dense clusters. On excavation, these prove to be derived from a complete inflorescence which is buried whole in the sand. Seedlings of *Ammophila* rarely survive in the foreshore at St. Cyrus and the mortality in all species is high.

Foredunes (*Stage B*).—Small hillocks of sand reaching about 9 inches develop around the species colonising the foreshore. These are normally blown away during the following winter, except where colonies of *Agropyron junceum* have become established. As these colonies enlarge in succeeding years, embryonic dunes form, young examples of which can be seen in the areas of two-year-old colonisation at the front of the dune ridge. Later these merge into undulating foredunes covered with a dense stand of *Agropyron*. Examples at this stage, reaching a height of 2 feet or more, occur at the southern tip of the dunes. *Agropyron* now appears in about 99 per cent. of $\frac{1}{36}$ sq. m. samples and few of the associated species occur in any abundance. Most of the species of stage A persist; *Ammophila arenaria* increases slightly in importance, and some others, including *Festuca rubra* var. *arenaria* and *Rumex crispus*, enter spasmodically. As seen from Table IV, 29 species are recorded from the foredunes.

Mobile and Young Fixed Dunes (*Stage C*).—When sand accumulation has reached 2 feet or more in height, *Ammophila arenaria* (hitherto showing frequencies of less than 10 per cent. in $\frac{1}{36}$ sq. m. samples) achieves dominance, with frequency figures about 98 per cent.

Agropyron decreases to about 4 per cent. and before long disappears entirely. As a result of the stout tussock-forming habit of *Ammophila*, coupled with the rhizome spread and vigorous sympodial vertical development, sand accumulation reaches its maximum in this stage, giving rise to the main dune ridge. Species of different growth-form, notably grasses, rosette plants, species with creeping stems and mosses, commence the stabilisation of the sand surface between the groups of *Ammophila* shoots. The most important of these are *Festuca rubra* var. *arenaria* (23 per cent.), which is a very characteristic associate of *Ammophila* in this stage, *Senecio jacobaea* (5 per cent.), *Cirsium arvense* (3 per cent.), and *Symphytum officinale.* Other entrants which play a significant part later are *Poa pratensis*, *Arrhenatherum elatius*, *Taraxacum officinale*, *Ononis repens*, *Ranunculus repens* and *Galium verum.* Although present throughout the succession from stage B, *Cerastium tetrandrum* is most abundant and best developed in stage C, while *C. vulgatum* also appears. Among the mosses the chief colonisers are *Bryum pendulum*, *Tortula ruraliformis* and *Ceratodon purpureus.* In all, 54 species of flowering plants are recorded.

Older Fixed Dunes (*Stage D*).—This stage is distinguished from the early fixed dunes by the closure of the community and the assumption of dominance by *Ononis repens*, which occurs in 91 per cent. of $\frac{1}{36}$ sq. m. samples. *Ammophila* is still an important constituent, but, besides dropping to a frequency of about 60 per cent., is reduced in vigour. A varied flora of 66 species is represented, in which turf-forming grasses are prominent, especially *Festuca rubra* (var. *arenaria* giving place to other forms), *Poa pratensis*, *Holcus latatus*, *Arrhenatherum elatius* and *Dactylis glomerata*, along with *Trifolium repens.* Some representatives of earlier stages, such as *Cirsium arvense*, *Cerastium tetrandrum*, *C. vulgatum* and *Senecio jacobaea*, retain an important place, while *Carex arenaria* appears, especially at the northern end of the dunes. Other species are *Galium verum*, *Veronica chamaedrys*, *Plantago lanceolata*, *Carlina vulgaris*, *Myosotis arvensis*, *Cerastium semidecandrum*, *Thalictrum arenarium* (locally dominant), while there is a strong representation of species of a taller growth-form, including *Solidago virgaurea*, *Campanula glomerata*, *Heracleum sphondylium* and *Valeriana officinalis* (locally dominant). The orthotropic mosses of stage C remain, while plagiotropic species such as *Brachythecium albicans* and *Hylocomium squarrosum* become increasingly prominent.

Dune Pasture (*Stage E*).—The later stages of fixation gradually give place landwards to a flat area of dune pasture. Although still present, *Ononis repens* and *Ammophila arenaria* are reduced to frequencies of 28 per cent. and 10 per cent. respectively, the *Ononis* remaining as scattered shoots of small size in the turf. Small clumps of degenerating *Ammophila* shoots mark the situation of former tussocks. Over large parts of the area *Carex arenaria* is dominant, and elsewhere a mixture of grasses forms a dense turf, including *Festuca ovina*, *F. rubra*, *Koeleria gracilis*, *Anthoxanthum odoratum*, *Helictotrichon* (*Avena*) *pubescens*, *Poa pratensis*, *Arrhenatherum elatius*, *Dactylis glomerata* and *Holcus lanatus*. Other abundant species among the 92 recorded from the dune pasture are *Galium verum*, *Veronica chamaedrys*, *Achillea millefolium*, *Campanula rotundifolia*, *Hieracium pilosella*, *Plantago lanceolata*, *Solidago virgaurea*, *Thymus serpyllum* agg., *Trifolium repens*, *Polygala vulgaris* and *Euphrasia officinalis* agg. Bracken is actively invading the dune pasture from the foot of the cliffs, and one dune pasture species—*Coeloglossum viride*—formerly restricted to this part of the area seems to have disappeared in recent years. In addition to bracken the list includes one other fern—*Botrychium lunaria*—and 20 bryophytes. The robust plagiotropic species *Hylocomium splendens*, *H. squarrosum* and *H. triquetrum* are frequent or abundant, while in the shorter turf occur *Dicranium scoparium*, *Polytrichum juniperinum*, *Climacium dendroides* and the mat-forming *Hypnum cupressiforme*.

Succession and the Rôle of certain Species.

The general nature of the succession at St. Cyrus is similar to that described under atlantic conditions in Harris, except that the following features suggest that, in the former locality, conditions change rather more rapidly. Certain species recorded only from dune pasture in Harris here enter at stage D or earlier, e.g., *Lotus corniculatus*, *Holcus lanatus*, *Achillea millefolium*, *Arrhenatherum elatius*, *Rhinanthus minor*, while *Ammophila arenaria* shows signs of declining at stage D whereas in Harris this did not occur until stage E, suggesting an earlier stabilisation of the sand surface and formation of a turf.

Active colonisation of the foreshore and development of foredunes has been observed but, owing to the longer periods of time involved, no direct evidence is available that the communities of the early and later fixed dunes and of the dune pasture represent stages in an active process of succession. That this is in fact the case, however, is strongly suggested by the following observations:

(*a*) the regular arrangement of the zones occupied by these communities passing landwards from the shore; (*b*) the gradual transition between each community; (*c*) the presence of the dominants and other important species of each as colonisers in the adjacent community on the seaward side and the degenerating condition of the same species in communities on the landward side; (*d*) the influence of the dominant species on the habitat.

Development beyond the stage of dune pasture is probably prevented by the intensity of rabbit grazing. Scattered specimens of *Crataegus monogyna*, *Rubus fruticosus* agg., *Rosa canina* agg., *Ulex europaeus* and *Acer pseudo-platanus* in the dune pasture indicate potentialities for further development, but the later stages in succession are considerably modified by the activity of rabbits. Some of the grass-dominated parts of the dune pasture are severely grazed to ground level, although a higher stand persists where the dominant is the less palatable *Carex arenaria*. Besides the grasses and some other herbs, *Ononis repens* is sometimes taken by rabbits and they are probably the chief agents in preventing shrub colonisation. In particular, *Ulex europaeus* is closely grazed and often reduced to a compact dome-shaped habit. Very young shoots of *Ammophila* appear to be palatable.

Rôle of Agropyron junceum.—A detailed investigation of the behaviour of *Agropyron junceum*, carried out by Mr. I. A. Nicholson, has clearly demonstrated that colonies of this species give rise to the first permanent accumulations of sand in the colonisation of the foreshore. After the young seedling has become established, the earliest tillers to be found adopt a markedly prostrate habit, giving rise to a small rosette of shoots more or less closely adpressed to the sand. If several such seedlings develop close together, an interlocking network of shoots is soon formed, which gathers a low hummock of sand. Owing to the persistence of *Agropyron* these hummocks generally survive the storms of the following winter and increase during the second year. As the colony becomes more dense, the prostrate habit of the shoots is gradually lost and the typically uniform close stand of somewhat flexuous shoots develops at the same time as the original isolated hummocks of sand merge together, forming the first "embryonic dunes" of stage B. Horizontal rhizomes may spread 2–3 feet outwards from these embryonic dunes, generally turning upwards and forming a terminal shoot towards autumn. In the following year this gives rise to a prostrate rosette of tillers and develops as in the case of a seedling.

Within the embryonic dune the plants respond to further sand accumulation by repeated upward sympodial shoot development, and specimens have been excavated showing origin 6 feet below the present sand-level. It is suggested, however, that such development weakens the plant and the very uniform stand characteristic of stage B degenerates.

Rôle of Ammophila arenaria.—Young plants of *Ammophila* show an erect habit, and it is probable that for this reason they are less efficient as initial agents of sand accumulation when compared with the prostrate, interlocking shoots of *Agropyron* (except possibly in regions of high winds and extensive sand movement, as in Harris where *Ammophila* initiates dune formation). Later, however, when the dense tufts of tall, rigid leaves invade the now erect stands of *Agropyron* and gradually give rise to large tussocks, the relationship is reversed. Sand accumulation is accelerated by *Ammophila*, and the plant appears to be in no way weakened by extensive vertical growth as the main dune ridges develop. These factors are probably operative in the replacement of *Agropyron* by *Ammophila* as the chief agent of dune formation (stage C), the former remaining for a time as a rather weak associate.

The behaviour giving rise to development of the tussock habit in *Ammophila* has been described by Greig-Smith *et al.* (1947), and the same features are seen at St. Cyrus, though not so conspicuously, possibly owing to the more rapid onset of degeneration. Causes of degeneration are unknown, but in this area the process may be hastened by rabbits.

Rôle of Mosses.—In the early phases of stage C, where *Ammophila arenaria* is most vigorous and sand movement is still considerable, there is little colonisation of the sand between the groups of *Ammophila* shoots. Towards the top of the ridge, however, and on the landward side where *Ammophila* seems to have reached the limit of its development, several mosses appear, first in small clumps, later becoming more widespread. Three species are important, all of a short erect habit, forming dwarf turfs with dense rhizoid development just below the sand surface. The first to establish itself is *Bryum pendulum*, often as a rather open turf of loosely arranged shoots, later becoming more compact and similar in growth-form to *Tortula ruraliformis* and *Ceratodon purpureus*, which soon become abundant. These species have been shown experimentally to be capable of growing up through at least 4 cm. of sand after sudden burial. By repeated development of shoots above and rhizoids below the sand surface they probably add considerably to the influence of the various colonists in reducing surface movement of sand and in increasing the moisture content and organic matter of the surface layers.

In addition to the forms mentioned, species of a low-growing plagiotropic habit enter at a slightly later stage, giving rise to compact mats over small areas. Such species as *Brachythecium albicans* become more prominent on passing into the closed community dominated by *Ononis repens* (stage D), while there is a reduction in the proportion of erect types and *Bryum pendulum* rapidly disappears.

In this zone the part played by bryophytes is largely complementary to the phanerogams in filling the available areas otherwise left bare and thus hastening the development of a compact turf. They are also complementary in a seasonal sense, since the luxuriant bryophytic growth is particularly obvious in spring before vegetative growth is much advanced in other plants, and in late autumn (October) after such species as *Ononis repens* have died back. The more robust and spreading forms become increasingly prevalent as components of the dune pasture.

Rôle of Ononis repens.—The behaviour of *Ononis* forms a parallel with *Agropyron junceum* in that the earliest entrants in the sequence, colonising stage C amongst the shoots of *Ammophila*, adopt a prostrate habit. The shoots radiate from the crown and become more or less dorsiventral in appearance, turning upwards at the tips only. Circular patches, sometimes over 2 feet in diameter, are formed in this way, and doubtless contribute to the stabilisation of the sand surface. Once established, however, *Ononis* spreads rapidly, the community becomes almost closed and dominance passes from *Ammophila* to *Ononis*. Under these conditions (regarded as characteristic of stage D) the shoots of *Ononis* are erect, standing about 8 inches high, with the leaves retaining their radial arrangement. Beneath the surface there is considerable rhizome development. The establishment of a closed community is reflected in an increase in the relative humidity of the air-layer at ground level and a higher moisture content in the surface layers of sand. In addition, the abundant root-nodules presumably enrich the nitrogen content of the sand, while the great depth of the root system (over 6 feet) probably ensures a more adequate water supply.

Rôle of Grasses.—Apart from the dominants already discussed, the only grass playing any part in the earlier stages of colonisation is *Festuca rubra* var. *arenaria*. In the later phases of stage C, just before *Ononis* begins to form a closed cover, *Poa pratensis* becomes established and contributes markedly in the initial stages of turf formation. *Holcus lanatus* comes next, followed by *Arrhenatherum elatius* and, to a lesser extent, by *Dactylis glomerata.* These are the main species giving rise to a compact turf, thus increasing the retention of moisture in the surface layers of the sand. The abundant production of fibrous roots in the top 6 inches of sand completes the binding process and adds to the organic content. The species of stage D retain their importance in the dune pasture (stage E) and are augmented by others such as *Festuca ovina, Koeleria gracilis, Anthoxanthum odoratum* and *Helictotrichon* (*Avena*) *pubescens.* As *Ononis* decreases, *Trifolium repens* becomes the prominent legume of the pasture.

Soil.

Analyses were made of certain of the physical and chemical factors in the substratum at each stage to record some of the changes which accompany the progress of succession. The results of these analyses may be regarded as illustrating stages in the development of a soil from bare sand.

Moisture Content.—Owing to the porous nature of the material and the free drainage there is great variability in moisture content especially at the surface. In relation to plant colonisation and succession, however, the amount of moisture retained at the surface in comparison with that at lower levels is significant. A set of samples at depths of 0 (surface sand), 3 inches, 6 inches, 9 inches and 12 inches were taken from each successional stage during dry weather (3rd July 1948), and the moisture content determined by oven drying at 100° C. The values for the 12-inch depth did not vary greatly throughout the sequence and there were no regular differences between this level and the intermediate depths. The differences in the conditions at the various stages are therefore indicated simply by expressing the moisture content in the surface sand as a percentage of that in the 12-inch sample (Table VI), and

TABLE VI.

MOISTURE CONTENT OF SURFACE SAMPLE AS PERCENTAGE OF THAT OF 12-INCH SAMPLE.

Stage:	A.	B.	C.	D.
	8·4	21·4	65·9	113·2

the increase in moisture retention at the surface as the succession proceeds is clearly demonstrated.

The variation of the moisture content at the surface may be seen in Table VII, which gives a selection of the data from weekly records made throughout 1949.

TABLE VII.

MOISTURE CONTENT OF SURFACE SAND EXPRESSED AS PERCENTAGE OF DRY WEIGHT.

Stage.*	Max.	Date.	Min.	Date.	Examples from Wet Period.		Examples from Dry Period.	
					Mar. 6.	Oct. 2.	June 19.	July 10.
A	11·8	Nov. 26	0·3	July 10	5·6	6·9	0·4	0·3
C	17·6	Nov. 26	0·3	June 29	5·6	6·5	2·1	0·5
D	36·6	Nov. 13	0·9	June 23	13·7	11·1	3·2	1·5
E	34·2	Jan. 15	1·9	July 30	32·7	30·1	7·4	3·0

In the early stages moisture at the surface never reaches a very high level and may fall very low. In stage A as high a value as 14 per cent. has been obtained immediately after rain, but except in continuously rainy weather only the top $\frac{1}{2}$–$\frac{3}{4}$ inch of sand is wetted and this dries out rapidly in direct sun. In the later stages of succession both the maxima and minima are higher.

The gradient of increasing values from A to E shown in the examples is not always so clearly marked, but there is a regular and characteristic increase on passing from C to D, so that A and C taken together stand out as distinct from D and E. This is evident at all times of the year, especially during wet weather, and is closely associated with the change from the open community in the earlier stages to the final stage represented by closed turf.

Standing water is reached between 6 and 8 feet below the surface in the foreshore and embryonic dune areas (A and B), but elsewhere no standing water was reached even at depths of 10 and 12 feet.

Salt Content.—The salt content of a similar set of samples was measured by extracting air-dry sand with distilled water and titrating with dilute silver nitrate. Table VIII shows that the amounts involved are relatively small, and that only the surface layers in the early stages are appreciably influenced. Presumably a certain amount of salt is deposited on the surface from spray, but the quantity diminishes as distance from the sea increases and it would appear that a very much smaller proportion of spray is arrested by the dunes than by parts of the cliffs. Further, any salt present in the sand will be rapidly leached out.

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* The samples were taken along a transect in which stage B was not represented.

TABLE VIII.

SALT CONTENT OF SAND EXPRESSED AS G. NACL/100 G. AIR-DRY SAND.*

Depth.	A	B	C	D	E
Surface	0·04	0·03	0·02	+	+
3 in.	+	+	0·02	+	+
6 in.	0·02	+	+	+	+
9 in.	+	+	+	+	+
12 in.	+	+	+	+	+

These results are at first sight surprising, owing to the proximity of the dunes to the sea, but are reflected in the fact that the foreshore community alone contains a halophytic element.

The physiological influence of salt depends on the amount of moisture present in the sand, but owing to the variability of this factor a table showing the concentration of salt in sand moisture in any particular set of samples would be valueless. It has been shown, however, that the sand surface dries out more frequently and more completely in the earlier stages, and the influence of salt will consequently be more pronounced there than in later stages.

Carbonate Content.—The percentage of calcium carbonate in a number of samples was determined by treatment with hydrochloric acid and back-titrating with sodium hydroxide (Piper, 1942). The carbonate content is not high, the mean value of samples from the top 12 inches of sand being only 1·75 per cent. There is, however, considerable variation between the samples (see Table IX).

The general means indicate a decrease as succession proceeds. This is doubtless a result of leaching, and in this respect St. Cyrus dunes show greater similarity to other dunes with low carbonate levels, *e.g.* Southport (Salisbury, 1925), than to those with high

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* Means from samples taken along three transects from which uniformly consistent results were obtained. The method was not regarded as sensitive enough to distinguish between values less than 0·02, which are therefore indicated by +.

TABLE IX.

CARBONATE CONTENT OF SAND EXPRESSED AS G. $CaCO_3$/100 G. AIR-DRY SAND.

Stage.	Depth.	Samples.			Mean.	
		I.	II.	III.		
A	Surface.	0·95	3·85	2·60	2·47	2·61
	6 in.	2·75	2·25	3·60	2·87	
	12 in.	1·35	3·85	2·30	2·50	
B	Surface.	0·60	2·30	2·60	1·83	1·69
	6 in.	1·55	1·10	1·35	1·33	
	12 in.	1·70	1·70	2·35	1·92	
C	Surface.	1·35	1·65	1·40	1·47	1·59
	6 in.	1·35	1·65	1·65	1·55	
	12 in.	1·75	2·20	1·35	1·77	
D	Surface.	3·65	2·10	1·70	2·48	1·67
	6 in.	0·90	1·40	0·65	0·98	
	12 in.	1·50	1·50	1·60	1·53	
E	Surface.	. .	0·85	2·10	1·47	1·06
	6 in.	1·00	0·60	0·00	0·53	
	12 in.	1·05	1·25	1·60	1·30	

levels as in Harris, and North Cornwall (Hepburn, 1945). Differences between percentages at different depths are not so marked as in Harris, but there is evidence for downward leaching in the fact that values at 12 inches are in general higher than at 6 inches, while samples from greater depths (between 4 and 6 feet) gave values up to 5 per cent. Higher figures and greater variability are obtained in the surface samples than at other depths, thus reinforcing the conclusion based on the Harris data that the major factor influencing carbonate content is uneven renewal at the surface by the deposition of wind-blown sand, which may occur at any stage.

Organic Matter.—Consistent results were obtained when three sets of samples at various depths in the top 12 inches of sand were ignited for three hours. The mean values are given in Table X. The original figures have been corrected to allow for loss in weight due to evolution of CO_2 from $CaCO_3$.

The lowest mean is obtained from stage C in which there is the greatest accumulation of wind-blown sand. There is no significant increase in organic matter until the community becomes closed in stage D, after which there is a considerable increase in the dune pasture (E). These increases take place chiefly in the surface layers.

TABLE X.

LOSS ON IGNITION EXPRESSED AS G./100 G. OVEN-DRY SOIL.

Depth.	A.	B.	C.	D.	E.
Surface.	0·29	0·28	0·21	1·29	7·47
3 in.	0·16	..	0·00	1·00	1·49
6 in.	0·00	0·41	0·18	0·69	1·11
9 in.	0·31	0·00	0·15	0·40	0·86
12 in.	0·12	0·33	0·11	0·31	0·36
General Mean:	0·17	0·31	0·14	0·75	2·64

The values given in Table X agree well with those from similar successional stages in the data given by Salisbury for Blakeney

TABLE XI.

pH OF SAND SAMPLES.

Stage.	Depth.	Samples.				Mean.	
		I.	II.	III.	IV.		
A	Surface.	7·92	6·76	7·73	8·04	7·61	7·84
	3 in.	7·49	6·87	..	..	7·18	
	6 in.	7·45	7·55	8·42	8·06	7·87	
	9 in.	8·10	7·92	..	..	8·01	
	12 in.	8·44	8·52	8·08	8·08	8·23	
B	Surface.	6·66	7·08	7·79	7·79	7·33	8·09
	3 in.	7·88	6·62	..	..	7·25	
	6 in.	8·39	8·45	8·19	8·29	8·33	
	9 in.	8·24	8·57	..	..	8·40	
	12 in.	8·61	8·47	9·18	9·19	8·86	
C	Surface.	7·65	7·92	6·56	7·11	7·31	7·82
	3 in.	7·83	8·44	..	..	8·13	
	6 in.	7·98	8·52	6·64	7·68	7·70	
	9 in.	7·98	8·67	..	..	8·32	
	12 in.	8·17	8·62	7·29	8·14	8·05	
D	Surface.	7·52	7·70	7·49	6·59	7·32	7·81
	3 in.	7·81	8·11	..	..	7·96	
	6 in.	7·48	8·06	7·98	7·79	7·83	
	9 in.	7·95	8·11	..	..	8·03	
	12 in.	7·76	8·26	8·31	8·17	8·12	
E	Surface.	5·17	7·46	5·90	..	6·18	6·64
	3 in.	5·93	..	..	..	5·93	
	6 in.	6·43	7·57	6·68	..	6·89	
	9 in.	6·95	..	..	..	6·95	
	12 in.	6·66	7·77	6·56	..	7·00	

(1922) and Southport (1925). A young *Ammophila* ridge (*i.e.* stage C) in the latter locality showed a lower value than the embryonic dunes (*i.e.* stage B), providing a parallel to the sequence at St. Cyrus.

pH Values.—These were obtained by the glass electrode method, and the data for different depths of sand in the several stages of succession are given in Table XI.

The differences between stages and between depths are significant. The pH values reflect the combined effects of the leaching of bases and the increase of organic matter. There is thus a downward increase in every stage, and (with the exception of a high figure for B) a decrease in the general means from A to E. In the first two stages a higher value at the surface than at 3 inches may reflect the renewal of bases in wind-deposited sand. The change from a slightly alkaline to a slightly acid soil during the progress of succession is again more similar to conditions at Southport than in Harris.

Chemical Analysis.—The following general analysis (Table XII) on bulked samples from the top 12 inches of sand at each stage was carried out by Dr. Reith of the Macaulay Institute for Soil Research.

TABLE XII.

GENERAL ANALYSIS OF SAND SAMPLES.
MG./100 G. AIR-DRY SAND.

Stage.	P_2O_5.	K_2O.	MgO.	MnO.
A	0·7	5·5	25	1·5
B	0·6	4·8	22	1·4
C	0·5	3·4	18	1·4
D	0·6	3·8	17	1·7
E	1·0	2·6	13	0·8

Table XII shows that, with the possible exception of magnesium, the concentration of minerals is low throughout the dune. In most cases there is a decrease throughout successive stages, possibly as a result both of leaching and of uptake by plants. There is an increase of phosphate, however, in the dune pasture.

Changes in the Habitat.

The preceding section indicates the changes taking place as a soil develops under the influence of the succession of plant communities. These changes may briefly be summarised as follows:

(i) An increase in the amount of moisture retained in the surface layers and a reduction in the rate of drying out.
(ii) Elimination of the influence of NaCl after stage A.
(iii) Leaching of carbonates and other minerals.
(iv) Increase in organic-matter content.
(v) Change from slightly alkaline to slightly acid.

In certain other ways, however, the succession gives rise to changes in habitat conditions, which in turn influence the composition of the communities. Firstly, the development of a dune ridge reduces the velocity of the wind affecting the landward regions of the area, especially in the case of winds blowing inland across the dunes. Relatively little wind-blown sand arrives in these regions (occupied by stages D and E), while other effects of wind exposure, such as evaporation or lowering of temperature in winter, are also reduced. Secondly, as a combined effect of reduced air movement and increased vegetational cover, the relative humidity of the air-layer in contact with the plants increases throughout the sequence. As measured by hygrometers placed in the vegetation, this gradient (Table XIII) is evident at all times of the year, although the general level of humidity varies.

TABLE XIII.

RELATIVE HUMIDITY OF AIR AT GROUND LEVEL IN DUNES.

Date: 1949.	A.	B.	C.	D.	E.
July 3 . .	50	62	79	83	84
September 30 .	63	67	74	82	91
December 4 .	85	. .	87	98	100

The general picture presented by the data given in the foregoing paragraphs is of a habitat which is highly exacting in the early stages, gradually ameliorating under the influence of a sequence of plant communities. This amelioration is evident both in changes in the substratum and in the atmosphere in the neighbourhood of the plants.

Subseres following Burning.

Fires are frequent on parts of the dunes and two distinct subseres have been identified, according to the stage of the community at the time of burning.

(i) *Burnt at Stage C.*—Permanent quadrats established after fires in areas occupied by stage C indicate that *Ammophila arenaria* regenerates rapidly, often within a single season. The pattern of the newly produced tussocks, however, seldom coincides with that of the old, and it is probable that regeneration is from rhizome buds or very young shoots which were below sand-level at the time of the fire. In less than a year, seedlings of *Senecio jacobaea* establish themselves, becoming extremely abundant in subsequent years. The first rosettes of *Cirsium arvense* occur after one year and later steadily increase in numbers. Patches of *Festuca rubra* are well established after two years, when some of the other species of stage C may reappear, such as *Solidago virgaurea* and *Myosotis collina*. Burnt areas, however, remain for a period of several years in a condition in which *Senecio jacobaea* and *Cirsium arvense* share dominance with *Ammophila arenaria*. Their further development is not yet known.

(ii) *Burnt at Stage D or E.*—Fires in areas previously occupied by these stages have left wide undulating regions in which, except occasionally in hollows, there is only a partial regeneration of *Ammophila*. A community of mainly dwarf plants, especially well developed on the sides of hummocks, is characteristic, having the following composition:—

Flowering Plants	
Festuca rubra	ld
Carex arenaria	la
Poa pratensis agg.	la
Sedum acre	la
Aira praecox	f
Cerastium semidecandrum	f
Cerastium tetrandrum	f
Senecio jacobaea	f
Taraxacum laevigatum	f
Taraxacum officinale	f
Arenaria serpyllifolia	o
Astragalus danicus	o
Carlina vulgaris	o
Erodium cicutarium agg.	o
Filago minima	o
Hieracium pilosella	o
Myosotis collina	o
Ononis repens	o
Phleum arenarium	o
Plantago coronopus	o
Plantago lanceolata	o
Senecio vulgaris	o
Solidago virgaurea	o
Vicia lathyroides	o
Arabis hirsuta	r
Centaurea nigra	r
Flowering Plants—*continued.*	
Erophila verna	r
Galium verum	r
Rumex acetosella	r
Sagina procumbens	r
Thymus serpyllum agg.	r
Mosses	
Ceratodon purpureus	d
Brachythecium albicans	ld
Hypnum cupressiforme	la
Tortula ruraliformis	la
Dicranum scoparium	o
Hylocomium squarrosum	o
Brachythecium purum	r
Bryum argenteum	r
Bryum pendulum	r
Lichens	
Cladonia cervicornis var. *subcervicornis*	d
Cladonia fimbriata	d
Cladonia foliacea	la
Cladonia rangiformis	la
Peltigera canina	la
Cladonia fimbriata f. *fibula*	o
Cladonia fimbriata var. *subulata*	o

The basis of the community over the greater part of the area is a co-dominance of *Ceratodon purpureus* with *Cladonia cervicornis* var. *subcervicornis* and *C. fimbriata*. This probably represents an early stage in colonisation following burning, and a later development is the entry of *Festuca rubra*. When the latter begins to become prominent, *Ceratodon* decreases, while *Sedum acre* takes an important place. Lichens remain abundant throughout, including *Cladonia rangiformis*, *C. foliacea* and *Peltigera canina* as well as those mentioned above. At this stage there is indication of an increase in *Carex arenaria*, and it is likely, though not proved, that a relatively stable *Carex*-dominated community would result. At no stage is *Ononis repens* observed to re-establish cover, although present in scattered patches.

The sequence outlined above is modified by areas in which *Brachythecium albicans* replaces *Ceratodon* as the colonising moss, a mixture of the two being comparatively rare. In these areas *Poa pratensis* is a more regular entrant, while *Hypnum cupressiforme* also contributes, sometimes resulting in the appearance of a *Poa-Hypnum*-Lichen associes in which *Brachythecium* is relatively insignificant.

The remaining species are widely distributed, many of them occurring in all the phases outlined above. Such species as *Aira praecox*, *Plantago coronopus*, *Phleum arenarium*, *Filago minima* and *Erodium cicutarium* give a characteristic facies to the burnt areas.

Colonisation near River-mouth.

At the southern limit of the dune ridge where it abuts on the mouth of the River North Esk, the foreshore and foredune communities contain an assemblage of ruderals, weeds, riverside species and tree seedlings. The species may be arranged in three groups as follows:—

(*a*) Species not recorded elsewhere on the dunes:

Aeschylus hippo-castanum *
Corylus avellana *
Fagus sylvatica *
Fraxinus excelsior *
Sambucus niger *
Agrostis stolonifera
Agropyron repens
Alchemilla vulgaris agg.
Chenopodium album
Lolium perenne
Luzula sylvatica
Matricaria maritima
Phalaris arundinacea
Polygonum aviculare agg.
Polygonum convolvulus
Polygonum persicaria
Scutellaria galericulata
Sinapis arvensis

(*b*) Species otherwise represented only at later stages of succession:

Acer pseudo-platanus *
Crataegus monogyna *
Rubus fruticosus *
Ulex europaeus *
Angelica sylvestris
Arrhenatherum elatius
Centaurea nigra
Chamaenerion (*Epilobium*) *angustifolium*
Dactylis glomerata
Festuca arundinacea
Filipendula ulmaria
Lotus corniculatus
Melandrium dioicum
Poa pratensis agg.
Rumex acetosa
Symphytum officinale
Trifolium campestre
Urtica dioica
Valeriana officinalis
Veronica chamaedrys

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* Seedlings.

(*c*) Species more numerous than in similar situations in other parts of the dunes:

Cerastium tetrandrum
Cirsium arvense
Cirsium vulgare
Holcus lanatus
Myosotis arvensis
Plantago lanceolatum
Potentilla anserina
Ranunculus repens
Rumex acetosella
Rumex crispus
Rumex obtusifolius
Senecio jacobaea
Sonchus asper

Quantitative analysis indicated that there was a concentration of individuals of these species in the sectors of the area closest to the river channel, and, although occurring for some yards inland of H.W.M., their density was greatest at the highest levels reached by tide debris. It is suggested that these plants may be derived from seeds floating downstream and becoming deposited on the dune on meeting incoming tides. They appear to find the conditions of early stages in the dune succession suitable for germination and seedling development, though those listed in group (*a*) and most of those in group (*b*) fail to persist for more than a year.

Discussion.

Three general points emerge from the results of this investigation. First, on comparing St. Cyrus with other dune systems, a section of the flora stands out as characteristic of the dune habitat, forming the basis of the vegetation. These species are common to most British dunes irrespective of local differences in climate and substratum, although very few are confined to dunes. From accounts of 15 dunes, Hepburn (1944) has drawn up a list of such species, of which over 60 per cent. are found at St. Cyrus.

The remaining portion of the flora will be determined by geographical and topographical situation and local conditions. That it is so rich and varied at St. Cyrus, as in certain other localities having favourable local climates, indicates that the succession may give rise to a habitat capable of supporting a community of relatively complex structure. The potentialities of this habitat are illustrated by the agricultural uses to which dune pasture areas have been put.

Secondly, emphasis has been placed on the fact that the sand-dune is an area of continuous change, such that the habitat occupied by dune pasture is developed from initial stages in which conditions are highly exacting. Much of the cause of this change can be found in the behaviour and reactions of the dominant plants, together with certain prominent subordinates. The effects are revealed in the changes and development of the remainder of the community. Accounts of dune vegetation are incomplete without reference to this aspect, and floristic comparisons are not valid unless the number of stages included in the analysis and the extent of development are known. Similarly, records of soil factors such as pH and carbonate content when given as averages for a whole area are of little value, since not only may there be considerable change through the sequence of stages, but there are also differences related to depth. A slight unbalancing of sampling in any direction may affect the results considerably. Thus it is especially important in the case of sand-dunes to relate the plant community to the analysis of the habitat at every sampling station.

Finally, as mentioned by Hepburn, comparisons of sand analyses from different areas indicate that two types of habitat may be recognised in British dunes. To the first belong those having very high percentages (often over 50 per cent.) of carbonate, and, in these, pH values and carbonate content are little affected by leaching. The second type, to which St. Cyrus belongs, is composed of sand with a much lower percentage of carbonate, generally below 10 per cent. and frequently less than 5 per cent. Here the progressive effects of leaching are clear, and in many cases the later stages are characterised by an acid soil.

While there is little difference in the basic flora of these two types, the additional species may reflect the composition of the substratum and the direction of succession may differ. The distinctions are to be seen more in the quantity of certain species and their relative contributions to the community, rather than in floristic differences, since many species traditionally regarded as calcicolous occur in both types. A clearer distinction is perhaps afforded by the bryophytes (e.g. *Camptothecium lutescens* tends to take the place of *Brachythecium albicans* on some of the highly calcareous dunes), and by the relative importance of lichens, which tends to be greater on the less calcareous dunes.

Summary of Part II.

An account is given of the vegetation of the dune ridge and dune pasture under the headings: (A) Foreshore colonisation, (B) Foredunes, (C) Mobile and young fixed dunes, (D) Older fixed dunes, (E) Dune pasture. Evidence is presented for regarding these as stages in an active process of succession.

Many of the causes of the initiation and progress of this succession are traced to the behaviour of the dominant species and certain prominent subordinates. Short accounts are given of the parts

played by *Agropyron junceum*, *Ammophila arenaria*, mosses, *Ononis repens*, and various grasses.

Parallel to the sequence of plant communities, changes in habitat conditions are observed. Comparative data for moisture content, salt content, carbonate content, organic matter, pH and the amounts of certain mineral salts illustrate the early stages in the development of a soil from sand. Moisture retention at the surface increases as succession proceeds; NaCl ceases to be significant after stage A; there is evidence of leaching of carbonates and other minerals; organic matter accumulates; and pH shifts from slightly alkaline to slightly acid.

The later stages are less subject to the influence of wind, and the relative humidity of the air-layer in contact with the vegetation is high. In general, changes in the habitat consist in the amelioration of an initially highly exacting environment.

Two subseres following fire are recognised, the differences between them being related to the stage reached by the vegetation prior to burning. A note is given on the colonisation of an area close to the river-mouth by ruderals, weeds, river-side species and tree seedlings.

St. Cyrus dunes, having an average $CaCO_3$ content of 1·75 per cent., are linked with certain other dunes having low carbonate levels, and contrasted with a group in which the substratum is highly calcareous.

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APPENDIX.

FLORISTIC LIST FROM CLIFF AND DUNE AREAS.

C—Recorded for main cliffs; S—Recorded for stacks;
D—Recorded for sand-dunes.

Dicotyledons.

Acer pseudo-platanus L.	C		D
Achillea millefolium L.	C	S	D
Agrimonia eupatoria L.	C		
Ajuga reptans L.	C		
Alchemilla vulgaris L. agg.	C		D
Anagallis arvensis L.	C		
Anchusa sempervirens L.	C		
Angelica sylvestris L.	C		
Anthriscus sylvestris (L.) Hoffm.	C		
Anthyllis vulneraria L.	C		D
Arabidiopsis (Sisymbrium) thaliana (L.) Heynh.	C		
Arabis hirsuta (L.) Scop.			D
Arctium lappa L.	C		D
Arenaria serpyllifolia L.	C		D
Armeria maritima Willd.	C	S	
Artemisia maritima L.		S	
Astragalus danicus Retz.	C	S	D
Astragalus glycyphyllos L.	C		
Atriplex babingtonii Woods			D
Atriplex laciniata L.			D
Atriplex littoralis L.			D
Atriplex patula L.	C	S	
Bellis perennis L.	C	S	D
Cakile maritima Scop.			D
Campanula glomerata L.	C	S	D
Campanula rotundifolia L.	C		D
Cardamine hirsuta L.	C		
Cardamine pratensis L.		S	
Carlina vulgaris L.	C	S	D
Centaurea nigra L.	C		D
Cerastium semidecandrum L.	C		D
Cerastium tetrandrum Curt.	C	S	D
Cerastium viscosum L.	C		
Cerastium vulgatum L.	C	S	D
Chamaenerion (Epilobium) angustifolium (L.) Scop.	C		D
Chenopodium album L.			D
Chrysanthemum leucanthemum L.			D
Cirsium arvense (L.) Scop.	C		D
Cirsium vulgare (Savi) Ten. (*lanceolatum* (L.) Scop.).	C		D
Clinopodium vulgare L.	C		
Cochlearia officinalis L.	C	S	
Conopodium majus (Govan) Lor. & Barr.	C		
Crataegus monogyna Jacq.	C		D
Crepis capillaris (L.) Wallr.	C		D
Dianthus deltoides L.	C		D

Dicotyledons—*continued*

Digitalis purpurea L.	C		
Echium vulgare L.	C		
Epilobium hirsutum L.	C		
Epilobium palustre L.	C		
Epilobium parviflorum Schreb.	C		
Erodium cicutarium agg.	C	S	D
Erophila verna (L.) Chevall.			D
Eupatorium cannabinum L.	C		
Euphrasia officinalis agg.	C		D
Filago germanica (L.) L.	C		D
Filago minima (Sm.) Pers.			D
Filipendula ulmaria (L.) Maxim.	C		D
Fumaria officinalis L.	C		
Galium aparine L.	C		D
Galium cruciata (L.) Scop.			D
Galium saxatile L.	C		
Galium verum L.	C	S	D
Geranium molle L.	C	S	D
Geranium pratense L.	C		D
Geranium sanguineum L.	C		D
Geum urbanum L.	C		
Hedera helix L.	C		
Helianthemum nummularium (L.) Mill.	C		D
Heracleum sphondylium L.	C		D
Hieracium sp.	C		D
Hieracium pilosella L.	C		D
Hyoscyamus niger L.	C	S	
Hypericum hirsutum L.	C		D
Hypericum pulchrum L.			D
Hypericum quadrangulum L. (*tetrapterum* Fr.)	C		
Hypochoeris radicata L.	C		D
Lamium purpureum L.	C		
Lathyrus pratensis L.	C		D
Lathyrus montanus Bernh.	C		
Leontodon autumnalis L.			D
Linum catharticum L.			D
Lotus corniculatus L.	C	S	D
Lycopsis arvensis L.	C		
Matricaria maritima L.	C		D
Melandrium album (Mill.) Garcke	C		D
Melandrium dioicum (L.) Coss & Germ.	C		D
Mimulus guttatus DC.	C		
Myosotis arvensis (L.) Hill	C	S	D
Myosotis collina Hoffm.	C		D
Nasturtium officinale R. Br.	C		

Dicotyledons—*continued*

Ononis repens L.	C	S	D
Origanum vulgare L.	C		D
Papaver dubium L.	C	S	
Papaver somniferum L.	C		
Pimpinella saxifraga L.	C		D
Plantago coronopus L.	C	S	D
Plantago lanceolata L.	C	S	D
Plantago maritima L.	C	S	D
Plantago media L.	C		
Polygala vulgaris L.	C		D
Polygonum aviculare agg.			D
Polygonum convolvulus L.			D
Polygonum persicaria L.			D
Potentilla anserina L.	C	S	D
Potentilla erecta (L.) Räusch	C		
Primula veris L.	C		D
Primula vulgaris Huds.	C		D
(*P. veris* × *P. vulgaris*)	C		
Prunella vulgaris L.			D
Ranunculus bulbosus L.	C		D
Ranunculus repens L.	C		D
Rhinanthus minor agg.			D
Rosa canina L. agg.	C		D
Rosa spinosissima L.	C		
Rubus fruticosus agg.	C		D
Rubus idaeus L.	C		
Rumex acetosa L.	C		D
Rumex acetosella L.	C		D
Rumex crispus L.	C	S	D
Rumex obtusifolius L.	C	S	D
Sagina procumbens L.	C		D
Salsola kali L.			D
Saxifraga granulata L.			D
Scrophularia nodosa L.			D
Scutellaria galericulata L.			D
Sedum acre L.	C	S	D
Sedum album L.	C		
Senecio jacobaea L.	C	S	D
Senecio vulgaris L.	C	S	D
Sherardia arvensis L.	C		
Silene maritima (Hornem.) With.	C	S	
Silene nutans L.	C		
Sinapis arvensis L.			D
Solidago virgaurea L.	C	S	D
Sonchus asper (L.) Hill.	C		D
Sonchus oleraceus L.	C	S	
Stellaria graminea L.	C		D
Stellaria holostea L.	C		
Stellaria media (L.) Vill.	C		D
Symphytum officinale L.			D
Tanacetum vulgare L.			D
Taraxacum laevigatum (Willd.) DC.			D
Taraxacum officinale Weber	C	S	D
Teucrium scorodonia L.	C		D
Thalictrum arenarium Butcher	C		D
Thymus serpyllum agg.	C	S	D
Torilis anthriscus (L.) C. C. Gmel.	C		
Tragopogon pratensis L.	C		D

Dicotyledons—*continued*

Trifolium arvense L.	C		D
Trifolium campestre Schreb.	C		D
Trifolium dubium Sibth.	C		
Trifolium pratense L.	C		
Trifolium repens L.	C		D
Trifolium scabrum L.	C		
Trifolium striatum L.	C		
Tussilago farfara L.	C		D
Ulex europaeus L.	C		D
Urtica dioica L.	C		D
Urtica urens L.	C		
Valeriana officinalis L.	C		D
Valerianella locusta L.	C		D
Verbascum thapsus L.	C		
Veronica arvensis L.	C		D
Veronica beccabunga L.	C		
Veronica chamaedrys L.	C		D
Veronica hederifolia L.	C		
Veronica officinalis L.			D
Veronica serpyllifolia L.	C		
Vicia cracca L.	C		
Vicia lathyroides L.			D
Vicia sativa L.	C		
Vicia sepium L.	C		D
Vicia sylvatica L.	C		
Viola canina L.	C		
Viola hirta L.	C		D
Viola riviniana Rchb.	C		D
Viola tricolor agg.	C		D

Monocotyledons.

Agropyron junceum (L.) Beauv.	C		D
Agropyron repens (L.) Beauv.	C		D
Agrostis stolonifera L.	C		D
Agrostis tenuis Sibth.	C		D
Aira praecox L.			D
Allium vineale L.	C		
Ammophila arenaria (L.) Link.	C		D
Anthoxanthum odoratum L.			D
Arrhenatherum elatius (L.) J. & C. Presl.	C		D
Brachypodium sylvaticum (Huds.) Beauv.	C	S	
Bromus mollis L.	C		
Carex arenaria L.	C		D
Carex flacca Schreb.	C		
Carex hirta L.	C		
Carex pendula L.	C		
(*Coeloglossum viride* (L.) Hartm.)			D
Dactylis glomerata L.	C	S	D
Elymus arenarius L.			D
Festuca arundinacea Schreb.	C	S	D
Festuca ovina L.	C	S	D
Festuca rubra L.	C		D
Helictotrichon (*Avena*) *pratense* (L.) Pilger	C	S	D
Helictotrichon pubescens (Huds.) Pilger	C	S	D
Holcus lanatus L.	C		D
Juncus articulatus L.	C		

Monocotyledons—*continued*

Juncus effusus L.	C		
Koeleria gracilis Pers.	C	S	D
Luzula campestris (L.) DC.	C		D
Luzula sylvatica (Huds.) Gaud.			D
Orchis mascula (L.) L.	C		
Phalaris arundinacea L.	C		D
Phleum arenarium L.			D
Phleum nodosum L.			D
Poa pratensis agg.	C	S	D
Poa trivialis L.	C		
Puccinellia maritima (Huds.) Parl.	C		
Scilla non-scripta (L.) Hoffmgg. & Link.	C		D

Pteridophyta.

Botrychium lunaria (L.) Sw.			D
Dryopteris filix-mas agg.	C		
Pteridium aquilinum (L.) Kuhn.	C		D
Equisetum arvense L.	C		

Bryophyta.

Amblystegium filicinum De Not.	C		
Brachythecium albicans B. & S.	C		D
Brachythecium purum Dixon	C		D
Brachythecium rivulare B. & S.	C		
Brachythecium rutabulum B. & S.	C	S	D
Bryum argenteum L.	C		D
Bryum pendulum Schp.			D
Camptothecium sericeum Kindb.	C	S	
Ceratodon purpureus Brid.			D
Climacium dendroides W. & M.	C		D
Dicranum scoparium Hedw.			D
Eurhynchium praelongum Hobk.		S	D
Eurhynchium rusciforme Milde var. *atlanticum* Brid.	C		
Fissidens taxifolius Hedw.	C	S	
Grimmia apocarpa Hedw.	C	S	
Grimmia maritima Turn.		S	
Hylocomium splendens B. & S.			D
Hylocomium squarrosum B. & S.	C		D
Hylocomium triquetrum B. & S.			D
Hypnum cupressiforme L.	C	S	D
Hypnum falcatum Brid.	C		

Bryophyta—*continued*

Hypnum schreberi Willd.			D
Mnium cuspidatum Hedw.			D
Mnium rostratum Schrad.			D
Mnium undulatum L.			D
Phascum cuspidatum Schreb. var. *piliferum* Hook. & Tayl.	C		
Polytrichum juniperinum Willd.			D
Tortula muralis Hedw.	C		
Tortula ruraliformis Dixon	C		D
Trichostomum crispulum Bruch	C		
Trichostomum tortuosum Dixon		S	
Weisia viridula Hedw.			D
Zygodon stirtoni Schp.		S	
Cephaloziella starkii (Funck.) Schiffn.			D
Conocephalum conicum (L.) Dum.	C		
Frullania dilatata (L.) Dum.		S	
Lophocolea bidentata (L.) Dum.		S	D
Madotheca thuja (Dicks.) Dum.		S	
Metzgeria furcata (L.) Dum.	C	S	

Lichens.

Callopisma citrinum (Hoff.) Mass.		S	
Cladonia cervicornis (Ach.) Schaer. var. *subcervicornis* (Wain.) Wats.		S	D
Cladonia fimbriata (L.) Fr.			D
var. *subulata* (L.) Wain.			D
f. *fibula* (Ach.)			D
Cladonia foliacea (Huds.) Willd.			D
Cladonia rangiformis Hoff.		S	D
Diploicia canescens (Dicks.) Mass.		S	
Lecanora atra (Huds.) Ach.		S	
Lecanora sulphurea (Hoff.) Ach.	C		
Peltigera canina (L.) Willd.	C	S	D
Physcia fusca (Huds.) Wats.		S	
Physcia hispida (Schreb.) Frege var. *tenella* (Scop.) Wats.	C	S	
? *Placodium lobulatum* (Flk.) Flag.		S	
Ramalina scopulorum (Retz.) Ach.		S	
Xanthoria parietina (L.) Th. Fr.	C	S	
var. *ectarea* (Ach.) Oliv.		S	

FURTHER OBSERVATIONS ON THE VASCULAR PLANTS OF THE OUTER AND INNER HEBRIDES. By J. W. HESLOP HARRISON, D.Sc., F.R.S.

(Read by title, 15th June 1950.)

Since we commenced our work on the plants of the Outer and Inner Hebrides we have published four floras: (1) The Flora of the Isle of Raasay and of the Adjoining Islands of South Rona, Scalpay, Fladday and Longay (Proc. Univ. Durham Phil. Soc., ix, 260–304, 1937); (2) The Flora of the Islands of Rhum, Eigg, Canna, Sanday, Muck, Eilean nan Each, Hyskeir, Soay and Pabbay (*ibid.*, x, 87–123, 1939); (3) A Preliminary Flora of the Outer Hebrides (*ibid.*, x, 228–273, 1941); (4) The Flora of the Isles of Coll, Tiree and Gunna (*ibid.*, x, 273–308, 1941). To these we have added a series of supplements and papers dealing with special islands and areas. In the last of these (Trans. and Proc. Bot. Soc. Edin., xxxv, Part II, pp. 132–156) a much more detailed account of the flora of the Isles of Lewis and Harris is supplied. The present paper, likewise of the nature of a supplement, deals chiefly with the Isles of Coll and Tiree (v.c. 103), Rhum and Eigg (v.c. 104), but supplies some facts about the vascular plants of the Outer Isles (v.c. 110). It lists plants not reported previously from individual islands and vice-counties, and includes others already on record from the three vice-counties, but now discovered in new stations.

As usual we have to tender our thanks to the Research Committee of King's College (University of Durham) for its generous support.

Anemone nemorosa L.

Although we have reported this species from Cleadale and other stations on the Isle of Eigg, it was first noted in Rhum, in the Kinloch woods, in 1949.

Ranunculus bulbosus L.

Plentiful behind the dunes at Kilmory and Samhnan Insir, Isle of Rhum.

Trollius europaeus L.

On the limestone outcrops, Monadh Dubh, Rhum.

Fumaria officinalis L.

By a *lapsus calami*, this species, occurring rarely in fields in the west of Coll, was listed as *F. purpurea* in the Coll "Flora".

Nasturtium officinale R. Br.

All of the specimens examined critically on Coll, Tiree and Eigg belonged to this species; the recently detected *N. uniseriatum* Howard & Manton was not represented.

N. uniseriatum Howard & Manton

Another station for this plant in v.c. 110 is on marshy ground near Kyles Stuley, on the opposite side of the Isle of South Uist to the original Bornish locality.

Draba rupestris R. Br.

Discovered by Dr. H. R. Fletcher, who accompanied our 1947 expedition, on the Fionchra cliffs facing Orval, Rhum.

Cochlearia danica L.

On rocks at Kilmory, Rhum.

Arabidopsis Thaliana (L.) Heynh.

Behind Laig dunes, Eigg, on Bloodstone Hill, Rhum, and on a field edge, Ormaclett, South Uist (110).

Subularia aquatica L.

Quite common in Loch Fiachanis, Rhum.

Viola canina L.

Sparingly on the inland face of Balephetrish Hill, Tiree.

Melandrium dioicum (L.) Coss. & Germ.

The ecotypes of this species collected on Bloodstone Hill and Ruinsival, Rhum, bear a considerable resemblance to that occurring on Ceann a'Mhara, Tiree, but all differ from the Shetland form *zetlandicum* Compt. which I have growing alongside them. Eigg forms show some relationship to the Bloodstone Hill plant, although there seems to be some admixture with mainland strains. In the Outer Isles (110), Muldoanich plants resemble those from Rhum, whilst those from the cliffs in Hellisdale and near Unasary, South Uist, represent an ecotype quite distinct from all the others mentioned.

Silene acaulis (L.) Jacq.

When one of our parties reported this plant in 1939 from sea-level habitats in the Uig district of Lewis, the only other Outer Hebridean localities known to us were on the Barra Isles of Mingulay and Berneray; it can now be recorded from Hellisdale in the Beinn Mhor massif, Isle of S. Uist. In Rhum, where the species abounds, it descends to sea-level at many points.

Cerastium semidecandrum L.
Collected at the mouth of Glen Guirdil, Rhum.

Hypericum Androsaemum L.
Usually found on sea-cliffs, but occurring inland along the Allt Beinn nan Stac, Rhum; also found in a new Eigg station near Laig Bay.

H. quadrangulum L.
In addition to the localities listed in our 1941 publication, there can be added two further Tiree stations, Ceann a'Mhara and Balephetrish Hill.

H. elodes L.
Plentiful around and in Lochs Caol, Cnoc Ibrig, and a'Chapuill, Tiree.

Geranium Robertianum L.
Generally recognized as a shingle plant in the Western Isles; now reported from rock debris at the base of cliffs in the hazel copse on Mullach Mor, at an elevation of 1800 feet on Barkeval, on the Long Loch and on rocks near Harris, all on the Isle of Rhum.

Medicago lupulina L.
On paths, etc., Kinloch and Kilmory, Rhum.

Vicia Orobus DC.
On rocks, west of Totronald, Isle of Coll; new stations on Rhum are on Mullach Mor and in a gorge on Beinn nan Stac.

V. angustifolia L.
Discovered in 1947 on Balephetrish Hill, Tiree, and on the Laig dunes, Eigg, in 1949.

Potentilla sterilis (L.) Garcke.
Behind the farm near Laig Bay, Eigg.

Dryas octopetala L.
Noted in 1948–49 on the saddle between Askival and Trallval, Rhum—a new locality far from the original limestone stations.

Rosa spinosissima L.

The form *rosea* Koch grows on cliff ledges in the gorge on Balephetrish Hill, Tiree.

R. canina L.

Occurs as the var. *biserrata* Baker on Balephetrish Hill, Tiree. On the Isle of Harris (110) vars. *sphaerica* Dum. and *globularis* Dum. grow near Luskentyre, and vars. *cladoleia* Rip. and *Schlimperti* Hoffm. near Tarbert and in Lingadale. Var. *insignis* B. & C., collected from the Rudha na Roinne cliffs, is new to our Rhum list.

R. dumalis Bechst. (=*R. glauca* auct.).

The var. *subcristata* (Baker) H. Harr. was found on Balephetrish Hill, Tiree, and in Lingadale, Laxadale, Skeaudale, and near Seilebost, Harris, and the var. *Reuteri* God. near Tarbert, Luskentyre, and on Strone Scourst, likewise on Harris.

R. caesia Sm.; *R. dumetorum* Thuill.; *R. rubiginosa* L.

As the first two of these exist as derelict stocks in the Castle rose garden, all Rhum records of their various forms should be rejected; the same applies to *R. rubiginosa* of which a huge hedge grows in the grounds.

R. Sherardi Dav.

Typical forms were obtained near Luskentyre and Seilebost, South Harris.

Prunus spinosa L.

A single bush flattened on a rock near Samhnan Insir, and a thicket on the sea-cliffs, just to the north, provide the first Rhum records.

Geum rivale L.

In a sea gorge near the Welshman's Rock; the lowest station recorded for Rhum.

Fragaria vesca L.

Amongst rocks at 1800 feet on Barkeval, and along the Long Loch, Rhum; a new station for the Outer Isles exists along the second stream west of the Allt Volagir, South Uist.

Saxifraga platypetala Sm.

In ravines, etc. on Bloodstone Hill, Orval, Sron an t'Saighdeir, and Fionchra, Rhum.

S. tridactylites L.

In June 1947 the machair around Vaul Bay, Tiree, was red owing to the presence of this plant.

Epilobium obscurum Schreb. × *E. montanum* L.

In the Kinloch woods, Rhum.

Eryngium maritimum L.

In abundance on the dunes, machair and seashore, Balephuil, Tiree.

Carum Carvi L.

Rare in a grassy place near the Post Office, Rhum.

Oenanthe crocata L.

Along a little stream flowing down Balephetrish Hill, Tiree; also on Eilean nan Each (104).

Hedera Helix L.

On the Creag an Fhireoin, Isle of Coll.

Galium pumilum Murr.

Amongst the rocks on sandy ground behind the dunes, Kilmory, Rhum.

Sherardia arvensis L.

Abundant on bank-sides near Laig farm, Eigg; also on similar ground, Kilmory, Rhum.

Valeriana officinalis L.

On the south bank of the Guirdil Burn, Rhum, and along streams near Laig, Eigg.

Valerianella locusta L.

Not rare on the landward side of the Laig dunes, Eigg.

Antennaria hyperborea D. Don.

Scattered along the Barkeval ridge, on Ruinsival and at an elevation of 500 feet along the Long Loch, Rhum.

Gnaphalium sylvaticum L.

On the south side of Loch Eynort, South Uist (110).

Carduus crispus L.

Apparently extending its range on Tiree, for it has now been collected in the area between Ruaig and Miodar.

Crepis paludosa (L.) Moench.

Amongst rocks at the base of the waterfall on the Guirdil Burn; the first Rhum record.

Chrysanthemum segetum L.

Amongst oats near Kilmory and Kinloch, Rhum.

C. Leucanthemum L.

More widely spread on Tiree than supposed, and in huge numbers in the fields, etc. between Arileod and the Machair Mhor, Isle of Coll; common enough near Cleadale, Eigg.

Lactuca muralis (L.) Fresen.

Sparingly on the rocks near the Laig waterfall, Eigg; new to v.c. 104.

Sonchus oleraceus L. × *S. asper* (L.) Hill.

A plant, almost certainly of the parentage indicated, was found with the putative parents in a disused vinery at Kinloch, Rhum.

Pyrola media Sw.

When we revisited Coll in 1947 we discovered that the only known colony of *P. minor* had been burnt off. We therefore searched closely for more; our quest was unsuccessful, but we did find a new colony of the present species on Carnan Mora.

Lycopsis arvensis L.

In fields on Rhum.

Myosotis scorpioides L.

On a stream near Ceann a'Mhara, Tiree, and in a ditch near the old manse, Coll.

Calystegia sylvestris Roem. & Schult.

Plentiful, and no doubt introduced, near Kinloch, Rhum.

Scrophularia nodosa L.

At the mouth of a sea gorge, Creag na h'Iolaire, Rhum; first record for the island.

Digitalis purpurea L.

Very fine amongst bracken and on cliff ledges on the Isle of Ronay (110), lying between North Uist and Benbecula; the form is distinguishable from Durham plants. Plants with blood-red flowers occur on the Samhnan Insir cliffs, Rhum.

Veronica persica Poir.
On cultivated ground at the base of An Cnap, Tiree.

V. officinalis L.
More widely distributed on Tiree than supposed—An Cnap, Balephetrish Hill, Ceann a'Mhara; also growing on Husival Mor and Husival Beag, Isle of Harris.

V. aquatica Bernh.
On a stream running into Vaul Bay, Tiree; near Bornish Church and Loch Ard Vule, Isle of South Uist (110).

Melampyrum pratense Beauv.
The var. *montanum* Johnst. was detected on Bloodstone Hill, Rhum, in 1943, and the var. *ericetorum* D. Oliver along the shores of Loch Cliad, Coll, in 1947.

Pinguicula lusitanica L.
White-flowered examples of this species were collected in a bog on Beinn nan Stac, Rhum.

Mentha Alopecuroides Hull.
On the same sandy stream on Tiree as *Veronica aquatica*.

M. piperita L.
Found once near Balephuil, Tiree.

M. arvensis L.
In a field at Kilmory, Rhum.

Galeopsis speciosa Mill.
Amongst oats, Kinloch, Rhum.

Lamium hybridum Vill.
On waste ground near the sea at the end of the Kenovay road, Tiree.

Ajuga reptans L.
Additional localities on Rhum to that on Mullach Mor are situated near the waterfall, Glen Guirdil, and in Kinloch woods.

A. pyramidalis L.
On cliff ledges, Eilean nan Each (104), but rarely flowering.

Polygonum Convolvulus L.
Amongst corn, Kilmory, Rhum.

P. Hydropiper L.

Near Unasary, Isle of South Uist; not noted previously on the island.

Rumex domesticus Hartm.

On the coast, Welshman's Rock, Rhum.

Myrica Gale L.

Reported in our "Flora" to be totally absent from Rhum; nevertheless, this species may be recorded now as existing in two tiny patches on the north shore of Loch Scresort, Rhum.

Betula pubescens Ehrh.

The little birch copse along Loch Cliad, Coll, has been destroyed by post-war moorland firing. Recently, however, we have greatly extended its known range on the island by discovering well-grown trees on Ben Hogh and on the Druim Fishaig cliffs. Moreover, the tree is much commoner, and more widely distributed on cliffs and in ravines on Rhum than we had previously thought.

Quercus petraea (Mattuschka) Liebl.

In addition to stations formerly listed for Coll, we can mention others on the shores of Loch an Duin and on the cliffs above Loch a'Mhill Aird and Loch na Cloiche. On Rhum a number of fairly large trees, discovered in 1946 on the cliffs in the north-west of the island, have been blown down recently. That these trees were native has been proved by their supporting oak galls of various species.

Salix pentandra L.

In Kinloch woods, Rhum; covered by masses of the scale insect *Lecanium capreae.*

S. aurita L.

A new locality for this species on Tiree is Balephetrish Hill; a plant bearing intersexual catkins was discovered near Loch Ceann a'Baigh, Isle of South Uist, in 1949.

S. Caprea L.

One tree in Kinloch woods, Rhum.

S. arenaria L.

Abundant on sandy ridges near Kilmory, Rhum, where intersexual catkins occur commonly.

S. repens L. × *S. herbacea* L.

On a small hill south-west of Minishal, Rhum; only the male plant occurs.

S. phylicifolia L.

On a stream running down Fionchra into Glen Shellesder, Rhum.

S. herbacea L.

On Ben Tangaval, Isle of Barra (110).

Empetrum hermaphroditum Hagerup.

This recently recognized species is widely distributed on the mountains of Rhum from Sron an t'Saighdeir and Orval to Askival, Hallival and Sgurr nan Gillean. Lower down, about the 1000-foot contour line, east of Loch Coire nan Grund, it abounds with *Juniperus sibiricus* amongst the scattered rocks.

Spiranthes stricta Nils.

In 1947 this rare orchid occurred in its usual numbers on the Isle of Coll, where it was found even in the gutter alongside the Arinagour–Gallanach road. The only insect noted at its flowers was the Silver Y moth (*Plusia gamma*).

Anacamptis pyramidalis Rich.

Very plentiful on the Machair Mhor, Isle of Coll, and the adjoining dunes, and varying greatly in flower colour; this provides a new habitat for the species on the island.

Orchis mascula L.

Noted freely amongst rocks west of Vaul Bay and Balephetrish Hill, Isle of Tiree.

O. latifolia L. (sec. Pugsl.).

The var. *coccinea* Pugsl. is to be found behind the dunes at Kilmory, Rhum, and in similar places at Balevanish, etc., Benbecula (110). The typical plant grows in the damp fields north of Kinloch, Rhum.

O. latifolia L. × *O. purpurella* Stph.

On Ceann a'Mhara, Tiree, and near Kinloch, Rhum.

O. purpurella Stph.

Very common in 1947, 1948 and 1949 at Kilmory, Samhnan Insir and Kinloch, Rhum, as well as in the centre of Coll; in both of these islands we had regarded the plant as rare. It grows also on Eilean nan Each (104).

× *O. viridella* J. Heslop Harrison (= *O. purpurella* Stph. × *Coeloglossum viride* (L.) Hartm.).

In a dune slack behind Laig Bay, Eigg.

O. majalis Reich.

A small colony of this species, containing over a dozen plants, was observed in 1949 in the first field north of the burn near Kinloch, Rhum. Although this ground has been worked regularly at the correct time for many seasons, the plant has not been detected previously.

O. ericetorum Linton × *O. purpurella* Stph.

Near Kinloch, Rhum.

O. ericetorum subsp. *rhoumensis* (J. H. H.) Hesl.-Harrison

This new subspecies, described as *O. Fuchsii* subsp. *rhoumensis* by J. Heslop Harrison in 1949, seems best, in spite of its chromosome number ($2n=40$), placed under *O. ericetorum* ($2n=80$). Formerly regarded by us as endemic in Rhum, it has now turned up on Eigg and Muck. The Eigg and Muck forms, however, have much paler flowers, and display a narrower range of variation in their colour than do Rhum plants.

Gymnadenia conopsea (L.) R. Br.

A further Rhum locality for the Fragrant Orchid exists in the second field to the north of the Kinloch burn.

Leucorchis albida (L.) Schur.

In the same field as the preceding species.

Platanthera bifolia Rchb. f.

Not rare, even in the Castle grounds, on Rhum in 1947, and common enough on the Isle of Coll the same season; uncommon in Central South Uist in 1949.

P. chlorantha (Cust.) Reichb.

Abundant on Coll in 1947 and on Rhum in 1947 and 1948. It swarmed similarly in 1949 in the Loch Iasgair area of South Uist.

P. chlorantha (Cust.) Reichb. × *Coeloglossum viride* (L.) Hartm.

With the parents on a grassy slope above Loch Iasgair, Isle of South Uist.

Allium ursinum L.

A third Rhum station is in a gorge near the Welshman's Rock.

Scilla non-scripta Hoffm. & Link.

A second Tiree habitat is Balephetrish Hill. In the old station on Ceann a'Mhara it was found growing on the same cliff ledge as *S. verna.*

Juncus trifidus L.

On Ruinsival, Rhum.

J. tenuis Willd.

Found on a bare patch of ground behind a wall near Loch Caol, Tiree; new to v.c. 103.

Luzula pilosa (L.) Willd.

Near the Laig waterfall, Eigg, and along the south side of Loch Scresort, Rhum.

Potamogeton crispus L.

In spite of my statement on this periodical (xxxv, Part I, p. 19), we have collected this species in v.c. 104 in the Isle of Raasay.

Eleocharis uniglumis Schult.

Just east of Beinn nan Stac, Rhum.

Eriophorum latifolium Hoppe.

Local on wet gravelly ground on the lower eastern slopes of Hallival and on the southern side of Mullach Mor.

Carex lasiocarpa Ehrh.

Abundant in Loch Cliad, Isle of Coll.

Poa irrigata Lindm.

Discovered on Fionchra during our 1948 expedition by Dr. W. A. Sledge.

P. Chaixi Vill.

Very plentiful in some of the woods at Kinloch, Rhum.

Desmazeria loliacea (Huds.) Nym.

On the dunes on Laig Bay, Eigg.

Elymus arenarius L.

Locally abundant on the Balevanish dunes, Isle of Benbecula (110).

Osmunda regalis L.

Around Lochs Udemul and Rumalach, Isle of Scarp (110).

Hymenophyllum peltatum Desv.
On Husival Beag, North Harris.

Equisetum pratense Ehrh.
A small patch of this horsetail was observed in 1948 growing in the gorge of the Shellesder Burn, Rhum, just after the stream begins to run west; new to v.c. 104.

E. hyemale L.
A single clump was encountered along the Allt Beinn nan Stac, Rhum.

E. variegatum Weber & Mohr.
In addition to the station on sandy ground behind the dunes at Kilmory, another Rhum colony exists on bare ground at an elevation of 1200 feet on Barkeval.

NOTES ON SCOTTISH FUNGI. By R. W. G. DENNIS.

(Read by title, 18th January 1951.)

In connection with a visit to Scotland to attend the Callander meeting of the Cryptogamic Section of the Botanical Society of Edinburgh, I took the opportunity of making mycological collections in the Cairngorms and the West Highlands, the latter between the 2nd and 6th of October 1950. The fungi noted in the latter area are listed below, but it may be worth while also to place on record collections of two inoperculate discomycetes which appear to have been hitherto unrecorded in Britain. A further new record of considerable interest in the list below is *Geoglossum starbaeckii*, collected on the 2nd of October between Crianlarich and Tyndrum. *Cortinarius adalberti* J. Favre and *Tricholoma odoratum* (Cool) Konr. & Maudl., both new to Britain, were collected in Rothiemurchus on 20th and 24th September respectively.

FUNGI COLLECTED IN ARGYLL.

The numbers following the specific names refer to the localities, which are as follows:

1, Dorlin; 2, Salen; 3, Kinlochmoidart; 4, Ardshealach; 5, Glen Uig; 6, Castle Tioram; 7, Glen Borrodale; 8, Tyndrum.

Amanita muscaria (L.) Fr., 1; *rubescens* (Pers.) Fr., 1.
Lepiota amianthina (Scop.) Fr. 1.
Armillaria mellea (Vahl) Fr., 1.
Tricholoma terreum Fr. 1.
Clitocybe nebularis (Batsch) Fr., 2; *aurantiaca* (Wulf.) Studer, 1.
Laccaria laccata (Scop.) Cke., 1; *amethystina* (Vaill.) Cke., 1.
Hygrophorus cinereus (Fr.) Karst., 1; *chlorophanus* Fr., 1; *coccineus* (Schaeff.) Fr., 1; *niveus* (Scop.) Fr., 1; *pratensis* (Pers.) Fr., 1; *puniceus* Fr., 1; *laetus* (Pers.) Fr., 1; *nigrescens* Quél., 2; *psittacinus* (Schaeff.) Fr., 2.
Mycena alcalina Fr., 1; *filopes* (Bull.) Fr., 1; *galericulata* (Scop.) Fr., 1; *galopus* (Pers.) Fr., 2; *epipterygia* (Scop.) Fr., 2.
Omphalia umbellifera (L.) Fr., 2.

Lactarius blennius Fr., 1; *glyciosmus* Fr., 1; *mitissimus* Fr., 1; *subdulcis* (Pers.) Fr., 1; *torminosus* Fr., 1; *vietus* Fr., 1; *vellereus* Fr., 2.

Russula nigricans Fr., 2; *fellea* Fr., 2; *ochroleuca* Fr., 2; *fallax* (Fr.) Cke., 1; *fragilis* Fr., 1; *xerampelina* Fr., 1.

Cantharellus cibarius Fr., 1; *tubaeformis* (Bull.) Fr., 3.

Entoloma jubatum Fr., 1.

Nolanea staurospora Bres., 1.

Pholiota squarrosa Fr., on apple, 4; *mutabilis* (Schaeff.) Fr., 2.

Naucoria escharoides Fr., 1.

Flammula sapinea Fr., 1.

Inocyba geophylla (Sow.) Fr., 1; *petiginosa* (Fr.) Gillet, 2.

Galera hypnorum Fr., 1.

Cortinarius rigidus (Scop.) Fr., 1; *caninus* Fr., 2; *collinitus* var. *trivialis* (Lange), Henry, 2.

Stropharia semi-globata (Batsch) Fr., 5.

Coprinus plicatilis (Curt.) Fr., 5.

Hypholoma fasciculare Fr., 1.

Psilocybe semi-lanceata Fr., 1.

Panaeolus campanulatus (L.) Fr., 1.

Boletus bovinus (L.) Fr., 1.

Hydnum repandum (L.) Fr., 1.

Fomes fomentarius (L.) Fr., 1.

Polyporus betulinus (Bull.) Fr., 1; *radiatus* (Sow.) Fr., 1.

Clavaria rugosa (Bull.) Fr., 1.

Scleroderma aurantium Pers., 1.

Leotia lubrica Pers., 1.

Trichoglossum hirsutum (Pers.) Boud., 6.

Geoglossum nigritum Cke., 1; *glutinosum* Pers., 2; *fallax* Durand, 1; *starbaeckii* Nannf., 8.

Corynetes atropurpureus (Batsch ex Fr.) Durand. 1.

Cordyceps militaris (Fr.) Link, 3.

Corynella prasinula (Karst) Boud., 1.

Hyaloscypha hyalina (Pers. ex Fr.) Boud., 7.

Myriangium duriaei Mont. & Berk. on scale insects on alder, 1.

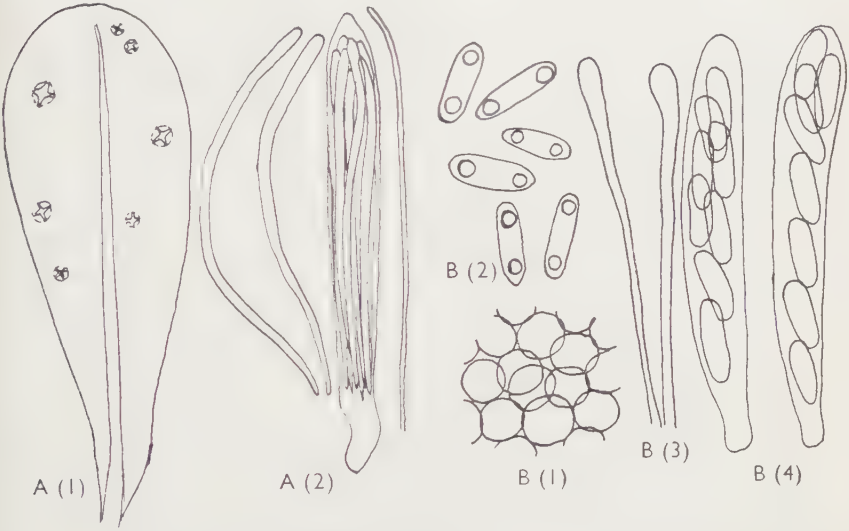
Rhytisma salicina (Pers.) Fr. on *Salix aurita* and *S. caprea*, 5.

Chlorosplenium aeruginosum (Oed.) de Not., 2 and 3.

Two Discomycetes new to Britain.

Pseudopeziza svalbardensis (Lind) Nannf. Nova Acta Soc. Sci. upsal. Ser. 4, VIII, 180 (1932). *Pyrenopeziza svalbardensis* Lind Skrifter om Svalbard og Ishavet, Oslo, No. 13 (1928).

Apothecia epiphyllous, circular, erumpent, disc dark brown, flat, about 400 μ diameter, with an erect, thin, blackish margin. Excipulum of isodiametric, thin-walled, dark brown cells 7–9 μ diameter. Asci cylindric-clavate, 8-spored, 60–70 × 10–12 μ, the pore not blued in Melzer's reagent. Spores irregularly biseriate, oblong with rounded ends, straight or slightly curved, hyaline, biguttulate, 12–17 × 4–6 μ. Paraphyses cylindrical, slightly thickened to 4–5 μ at the rounded apex.



A, *Stictis arctostaphyli*: (1) infected leaf (× 8); (2) ascus and spores (× 750). B, *Pseudopeziza svalbardensis*: (1) excipular cells; (2) spores; (3) paraphyses; and (4) asci (× 750).

In dark brown spots on leaves of *Saxifraga aizoides* about 2500 ft. Ben Lui, Tyndrum, 2.x.1950.

Lind described this species on *Draba wahlenbergii* and *Saxifraga hirculus* from Spitzbergen without designating a type. Nannfeldt (*op. cit.*) subsequently separated the form on *Draba* as *P. drabae* Nannf. and restricted *P. svalbardensis* to the form on *Saxifraga*. The Scottish material appears to differ from the type only in the spores not being one-septate. As it contains comparatively few mature asci, and spore septation in inoperculate discomycetes is a very inconstant character, no significance attaches to this discrepancy.

The same plants bore a few fructifications of a microthyriaceous fungus, apparently an undescribed species of *Stomiopeltis*.

Stictis arctostaphyli Ferd. & Winge. Bot. Tidsskr., xxviii, 253 (1907).
Naemacyclus penegalensis Rehm. Verh. bot. Ver. Brandenburg, 34 (1908).

Ascomata hypophyllous, erumpent, covered when dry by 3–5, usually 4, triangular lobes of the torn epidermis, disc grey, ½–1 mm. diameter. Asci cylindric clavate, 75–80 × 7–10 μ, somewhat pointed above, the pore not blued in Melzer's reagent, 8-spored. Spores cylindrical or tapering downwards, 60–70 × 2–2·5 μ. Paraphyses filiform, 1–1·5 μ thick.

On dead lower leaves of *Arctostaphylos uva-ursi*, Lochnagar, August 1945, Dr. H. F. Dovaston; Cairngorm at about 2500 ft., 28.ix.1950.

Some Fungi from Sutherland.

By F. L. Balfour-Browne.

(Read by title, 18th January 1951.)

With the exception of the rusts listed by Malcolm Wilson in Trans. Bot. Soc. Edin., xxxi, 345–449, 1934, practically no fungi have been recorded from the county of Sutherland. Stevenson in Mycologia Scotica, 1879, may have included some Sutherland fungi in his Ross references, where Ross is taken to include the south and west corner of Sutherland extending between Cape Wrath, Loch More, Oykel and the west coast. It is therefore thought to be of interest to record the few fungi found during a ten days' holiday in June 1948, spent at Lochinver and Inchnadamph. (Species included in Stevenson's Mycologia Scotica are indicated thus,*; the rest are recorded for the first time for Sutherland; † indicates a new record for the British Isles.)

Very few agarics were noted, doubtless due in part to the earliness of the season and in part to the subarctic moorland type of country, with only a rare tree on ground where the sheep cannot get a foothold, or with occasional small areas of scrubland, as for example by the shores of Loch Assynt. In such areas the fungus flora immediately becomes less sparse. R. W. G. Dennis, collecting in Ross the previous June around the more wooded Applecross and Gairloch, was more successful (Trans. Bot. Soc. Edin., xxxiv, 397–401, 1948).

To define the localities, the grid readings on the popular edition 1-inch O.S. maps, published in 1947, were taken—chiefly on sheet 15 of this set.

12.6.48: Lochinver—pools on the shore and above high water.
13.6.48: Loch Druim Suardalain, 110216; Loch na Circe, Canisp Forest.
14.6.48: Loch an Ordain, 065259; Loch na h Inghinn, 050265; Bay of Clachtoll, 040270; Bay of Culkein, 040330.
15.6.48: Loch Druim na h Uamha Moire, 226280; Allt Sgiathaig, 234274; Loch Assynt shore, 165254.
16.6.48: Alltpolt an Droighinn, 283238; Loch h an Ouaran, 290240; another, nameless, loch, 275244.

17.6.48: Conival, 3234 ft.
18.6.48: R. Traligill, Inchnadamph.
19.6.48: Unapool Bay, 229336.
20.6.48: Loch an Ais, 185093; a loch on Cromalt Hills, 195085. Both these sites are in Ross-shire.
21.6.48: Loch Broom, 151921.

The material collected is deposited in the British Museum (Natural History).

Hymenomycetes.

Amanita excelsa Fr. Loch Assynt among birch and willow.

* *Psalliota arvensis* Schaeff. ex Fr. Glen Canisp area at 700 ft.

* *Marasmius dryophilus* Bull. ex Karst. Loch Assynt.

* *Hygrophorus pratensis* Pers. ex Fr. A very small specimen, occurring about 100 ft. below the summit of Conival.

* *Omphalia fibula* Bull. ex Fr. Druim na h Uamha Moire and Inchnadamph.

Entoloma sericeum Bull. ex Fr. Inchnadamph forest area.

* *Galera hypnorum* Batsch ex Fr. Druim na h Uamha Moire.

* *Tubaria furfuracea* (Pers. ex Fr.) Gill. Glen Canisp forest at 700 ft. and at Inchnadamph.

Schizophyllum commune Fr. Loch Assynt.

Polyporus varius Fr. Loch Assynt.

* *Polyporus betulinus* Bull. ex Fr. Loch Assynt.

* *Polystictus versicolor* Linn. ex Fr. Loch Assynt.

Discomycetes.

Vibrissea truncorum Alb. & Schw. ex Fr. On roots of *Calluna*, at base of Suilven, 1000 ft. Salmon pink apothecia with blackish stalks.

Orbilia xanthostigma Fr. On fallen wood, Loch Assynt.

Chlorosplenium aeruginosum (Oeder.) de Not. On birch, Loch Assynt.

Dasyscypha virginea (Batsch ex Fr.) Fuckel. On fallen birch, Loch Assynt.

Micropodia arenula (Alb. & Schw. ex Fr.) Sacc. On *Pteris* fronds, Loch Assynt.

Mollisia cinerea (Batsch ex Fr.) Karst. On the cut end of a birch twig, Loch Assynt.

Pyrenopeziza arenivaga (Desm.) Boud. On *Phragmites communis* in Loch Druim Suardalain. Previously recorded only on

Psamma arenaria, but in spite of the difference in host and in the habitat of the host there seems to be no justification for describing this as new.

Niptera pulla (Phill. & Keith) Boud. On *Phragmites* in Loch Druim Suardalain.

Durella compressa Pers. ex Tul. On *Calluna* stems, Loch Assynt.

PYRENOMYCETES.

Hypoxylon multiforme (Fr.) Fr. Abundant on birch branches, Loch Assynt.

Mycosphaerella sp. indet. On *Dryas*, Traligill, near Inchnadamph. Only one ascocarp was found and the measurements did not agree with the species already described on this host. Further collections slightly later in the year are desirable.

Sphaerella epistroma Cooke. On *Molinia caerulea*, Loch Assynt.

Leptosphaeria culmifraga (Fr.) Ces. & de Not. On *Festuca*, Inchnadamph forest.

† **Pyrenophora venturia** (Speg.) Sacc. Syll. Fung., II, p. 280 (C. Spegazzini in Michelia, I, p. 461).

Perithecia 150–200 μ diameter, scattered, amphigenous but chiefly epiphyllous, globose or pyriform, with erect dark brown or black, acute, septate bristles, 50–120 μ × 4–7 μ. Asci cylindrical to clavate, four to eight spored, 80–100 μ × 20–40 μ. Ascospores broadly elliptical or boat-shaped, with ± obtuse ends and with five to seven transverse septa, often constricted at the fourth, and with two to three vertical septa, yellow to brown, 25–35 μ × 14–16 μ. Paraphyses not observed.

Hab. In dead leaves of *Dryas octopetala*, Traligill. A new record for Great Britain.

The Scottish fungus differs from the first described *P. venturia* from Italy in generally being epiphyllous and in its larger and septate bristles; the septa are, however, somewhat difficult to see owing to the dark colour of the bristles. Other characters are in close agreement.

Endodothiella junci (Fr.) Theiss. & Syd. On dead Juncus, Loch Assynt and Loch Broom.

FUNGI IMPERFECTI.

Phyllosticta ericae All. On dead sepals of *Erica cinerea*, Inchnadamph.

Actinothyrium graminis Kunze. On dead *Molinia caerulea*, Traligill and Loch Assynt.

Staganospora subseriata (Desm.) Sacc. var *moliniae* Trail. On dead *Molinia* leaves. Pycnidia not coalescing and conidia rather smaller than in *S. subseriata*.

† **Cercospora narthecii** sp. nov. On dead *Narthecium ossifragum*, Inchnadamph forest.

Fumago vagans Pers. ex Sacc. On leaves of *Arctostaphylos Uva-ursi*, Druim na h Uamha Moire.

Cercospora narthecii F. L. Balfour-Browne, sp. nov.

Conidiophores erect and tapering, fuliginous with lighter apices, septate, 100–150 μ × 5–6 μ, arising on a brown pseudoparenchymatous stroma. Conidia elliptical, hyaline to light olive, non-septate, abstricted terminally or laterally, occasionally in chains, 12–15 μ × 4–5 μ.

Hab. On dead flower spikes of *Narthecium ossifragum*, Inchnadamph forest.

Conidiophoris erectis, supra attenuatis, fuliginosis, apicis hyalinis vel dilutissime fumosis, septatis, 100–150 μ × 5–6 μ, ex stromatis brunneis et pseudoparenchymatis emergentibus. Conidiis ellipticis, continuis, hyalinis vel dilutissime olivaceis, apicalis vel lateralis, subinde catenulatis, 12–15 μ × 4–5 μ.

Hab. Ad scapos siccos Narthecii ossifragi.

Recent Additions to the Algal Flora of St. Andrews, Fife. By H. Blackler, Ph.D.

(Read by title, 18th January 1951.)

As a result of investigations on the algae on the shores of St. Andrews the following species have been found, which have not been recorded either by Lowe, 1935, or Dunn, 1939 and 1941.

Chlorophyceae.

1. *Endoderma Flustrae* (Reinke) Batters

Common on *Dynamena pumila* where it forms extensive patches colouring the colonies green.

2. *Tellamia contorta* Batters

3. *Tellamia intricata* Batters

Both species of *Tellamia* occur together in the periostracum of *Littorina littoralis* and *Littorina saxatilis*, which is coloured green by the algae. Previously recorded by Batters from the Cumbraes.

4. *Chaetomorpha litorea* (Harv.) Cooke

Occurs in pools.

5. *Chaetomorpha aerea* (Dillw.) Kütz.

This species was recorded for the Fife coast by Dr Trail at Elie, 1888.

6. *Gomontia polyrhiza* (Lagerh.) Born. & Flah.

Found on *Balanus balanoides*, which is coloured green with it in the winter months.

Phaeophyceae.

7. *Tilopteris Mertensii* (J. E. Smith) Kütz

Small oogonial plants found growing in sandy pools this June.

Rhodophyceae.

8. *Acrochaetium endozoicum* (Darb.) Batt.

Abundant in *Alcyonidium hirsutum*.

9. *Chromastrum secundatum* (Lyngb.) Papenfuss = *Acrochaetium secundatum* (Lyngb.) Naegeli

Epiphytic on *Porphyra umbilicalis* and *Cladophora rupestris* and other algae. Found at Elie by Trail.

10. *Laurencia obtusa* (Huds.) Lamour

11. *Pterosiphonia parasitica* (Grev.) Schmitz

Found growing in deep pools in the Laminaria zone. Recorded from Earlsferry, near Elie, by Trail.

12. *Rhodocorton purpureum* (Lightf.) Rosenv. *forma globosa* Kjellm.

This form grows on high rocks and cliffs in small nodules about the size of a pea, as described by Børgesen for similar habitats in the Faeroes, and agrees with his description in all respects. This form has been found in the Orkneys by Sinclair, but is not recorded from other localities in the British Isles.

13. *Harveyella mirabilis* (Reinsch) Schmitz and Reinke

Parasitic on *Rhodomela subfusca* where it forms small white hemispherical masses often in clusters.

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SPORE MORPHOLOGY IN BRITISH FERNS. By ELIZABETH M. KNOX, M.A., D.Sc. (With Plates XX and XXI.)

(Read by title, 18th January 1951.)

A recent attempt to determine the species represented by certain wind-blown spores collected in England revealed the lack of any complete account of the spore morphology in British Ferns. Moreover, in connection with the increasing attention which is being given to spore and pollen analysis of peat deposits in this country, the necessity for an illustrated description of the spores of ferns indigenous to Britain has become apparent.

The spores of certain species have been described and illustrated by various authors, including Hegi (1936), who gives figures for a number of British species, while general descriptions of spore structure characteristic of Fern families are given by Copeland (1947) and Holttum (1947). Since the available descriptions and illustrations are scattered through an extensive literature, it is hoped the following account will prove useful in the identification of fern spores which may be found in British peat deposits. The specific names used are those of the Check List of British Vascular Plants (Clapham, 1946), and, as far as possible, references to descriptions and figures by other authors are given under the several species. An exception is made, however, in the case of some of the older writers, *e.g.*, Hooker and Greville (1831), Hooker and Bauer (1842), Moore (1859), Fée (1854), and Milde (1865), since brevity of description and smallness of the illustrations given by these authors render them rather inadequate. Their figures are, therefore, not particularised here. The most useful account is to be found in the paper by Karpowicz (1927), but she does not include all the British species.

The Check List enumerates 45 species of British Ferns excluding so-called water ferns; the spores of each of these have been examined, described and illustrated with the exception of those where there is a close resemblance to a related species.

A uniform method of treatment and examination has been employed throughout. The spores were boiled for a few minutes in 10 per cent. KOH, washed in water and mounted in glycerine jelly.

On each slide not fewer than 10 spores were measured, and the average of the measurements as well as the range are recorded.

OPHIOGLOSSACEAE.

Botrychium lunaria (L.) Sw. (fig. 1).

Tetrahedral, rounded-triangular, average diameter 40·9 μ, ranging from 35–45 μ. Triradiate mark extending almost to the margin. On the ab-apical surface the exospore is ornamented with irregularly shaped, rather large, warty excrescences, 5–8 μ across, separated by winding channels. Round the apical crest the protuberances are smaller; the spore margin is crenate.

The spores of this species are described and figured by Karpowicz (1927, Pl. 2, fig. 6) and Erdtman (1943, fig. 472).

Ophioglossum vulgatum L. (fig. 2).

Tetrahedral, rounded-triangular to spherical, average diameter 41·3 μ, ranging from 36–45 μ. Triradiate mark $\frac{2}{3}$ radius. Exospore reticulate; mesh 5–8 μ, with prominent lamellae. The reticulum is less pronounced on the apical surface, round the apical crest.

The spores of this species are described and figured by Karpowicz (1927, Pl. 2, fig. 9).

Ophioglossum lusitanicum L. (fig. 3).

Tetrahedral, almost spherical, average diameter 38 μ, ranging from 35–40 μ. Triradiate mark $\frac{2}{3}$ radius. Exospore pitted; pits 2 μ across, irregular in shape and rather widely spaced 2–4 μ apart.

OSMUNDACEAE.

Osmunda regalis L. (fig. 6).

Tetrahedral, spherical, average diameter 64μ, ranging from 58–67μ. Triradiate mark $\frac{1}{3}$ radius. Exospore verrucose, being ornamented with very numerous irregularly shaped warty excrescences.

The spores of this species are described and figured by Leurssen (1889, fig. 33), Diels (1902, fig. 203), Karpowicz (1927, Pl. 2, fig. 10), and Hegi (1936, Pl. 1, fig. 25).

HYMENOPHYLLACEAE.

Hymenophyllum tunbrigense (L.) Sm. (fig. 4).

Tetrahedral, spherical, average diameter 32·4 μ, ranging from 30–35 μ. Triradiate mark extending to the margin. The delicate, thin-walled exospore is ornamented with triangular emergences about 2 μ long and set 3–5 μ apart, giving a denticulate appearance to the margin.

The spores of this species are briefly described by Hooker (1831), Moore (1859), and figured by Hegi (1936, Bd. 1, p. 7, fig. 1).

Hymenophyllum peltatum (Poir.) Desv. (fig. 5).

Tetrahedral, spherical, average diameter 58·7 μ, ranging from 54–68 μ. Triradiate mark extending to the serrulate margin. Exospore thin and bearing closely set, slightly obtuse processes, 2 μ long; the apical crest is scabriolate.

Trichomanes speciosum Willd. (*T. radicans* Sw.) (fig. 7).

Tetrahedral, spherical, average diameter 32·1 μ, ranging from 30–35 μ. Triradiate mark extending to the finely serrulate margin. Exospore thin and ornamented with numerous short, sharp, acicular processes, 1–2 μ long.

POLYPODIACEAE.

Pteridium aquilinum (L.) Kuhn (fig. 8).

Tetrahedral, subtriangular, with straight or slightly concave sides, average diameter 34 μ, ranging from 30–42 μ. Wall 1–2 μ thick. Triradiate mark extending almost to the margin. Exospore coarsely granulate. This species might be confused with *Adiantum capillus-veneris* (fig. 11), but the larger size and finer granulation of the latter are distinguishing features.

The spores of this species are described and figured by Karpowicz (1927, Pl. 2, fig. 11), Hegi (1936, Pl. 1, figs. 7, 8), Erdtman (1943, fig. 484), Selling (1946, fig. 103, and p. 48, where references are given to other figures), and by Gams (1948, fig. 179, 7).

Cryptogramma crispa (L.) Hook & Bauer (*Allosorus crispus* (L.) Bernh.) (fig. 9).

Tetrahedral, triangular with concave sides and prominent blunt corners, average diameter 54 μ, ranging from 47–60 μ. Triradiate mark extending to the margin. Exospore ornamented by low, rounded, more or less irregularly shaped bosses, averaging 5 μ in diameter and closely set together. Round the apical crest the elevations are smaller; the spore margin is crenate.

The spores of this species are figured by Hegi (1936, Pl. 1, fig. 3).

Anogramma leptophylla (L.) Link (*Gymnogramme leptophylla* (L.) Desv.) (fig. 10).

Tetrahedral, triangular with straight sides, corners rounded, average diameter 50 μ, ranging from 45–55 μ. Triradiate mark extending almost to the margin. Spore wall 3 μ thick. On the ab-apical surface the ornamentation is of low rounded elevations, irregularly shaped and closely packed together, similar to *Cryptogramma crispa* (fig. 9). The apical crest is coarsely papillate and bordered by two smooth ridges between which are long narrow furrows lying parallel to the sides of the spore. The ridges are about 5 μ in width.

The spores of this species are figured by Leurssen (1889, fig. 34) and by Hegi (1936, Pl. 1, figs. 4, 5, and 6).

Adiantum capillus-veneris L. (fig. 11).

Tetrahedral, sub-triangular with slightly convex sides, average diameter 44·5 μ, ranging from 40–47 μ. Wall 2 μ thick. Triradiate mark extending almost to the margin and bearing a conspicuous apical crest. Exospore finely granulate, margin entire.

The spores of this species are described and figured by Selling (1946, figs. 122–125, and on p. 52 further references are given to descriptions and illustrations).

Blechnum spicant (L.) Roth (fig. 12).

Bilateral, ovoid, average size 31 × 48 μ, ranging from 27–35 μ × 45–52 μ. Wall 2 μ thick. Longitudinal slit does not extend to the margin and frequently appears to be open. Exospore smooth with a thin, membranous perispore, which readily peels off.

The spores of this species are described and figured by Karpowicz (1927, Pl. 1, figs. 7 and 8), Hegi (1936, Pl. 1, figs. 19 and 20), and by Gams (1948, fig. 179, 3).

Phyllitis scolopendrium (L.) Newm. (*Scolopendrium vulgare* Sm.) (fig. 13).

Bilateral, bean-shaped to ovoid, average size 23 × 32 μ, ranging from 20–25 μ × 27–35 μ. Spore furnished with a thin perisporal membrane bearing irregularly shaped pointed processes.

The spores are described and figured by Karpowicz (1927, Pl. 2, fig. 12), Hegi (1936, Pl. 1, fig. 21), and by Gams (1948, fig. 179, 1).

Asplenium adiantum-nigrum L. (fig. 17).

Bilateral, ovoid, average size 28 × 36 μ, ranging from 25–32 μ × 33–40 μ. Spore with a deeply folded, winged perisporal membrane, projecting 5–7 μ beyond the margin of the spore and appearing as an irregular, sinuate border.

The spores of this species are described and figured by Karpowicz (1927, Pl. 1, fig. 4) and Hegi (1936, Pl. 1, fig. 9).

Asplenium marinum L. (fig. 14).

Bilateral, ovoid to almost spherical, average size 21·4 μ × 25·3 μ, ranging from 20–24 μ × 23–27 μ. Spore covered by a thin membranous perispore forming irregular folds and outgrowths, seen at the margin as pointed projections.

Asplenium obovatum Viv. (*A. lanceolatum* Huds.).

Bilateral, ovoid, average size 33·2 × 40·3 μ, ranging from 27–36 μ × 35–50 μ. Spore covered by a thin perisporal membrane, folded and wrinkled, extending from 5–7 μ beyond the spore surface and frequently exhibiting a fimbriate margin. In general appearance the spores are similar to those of *A. viride* (fig. 16).

Asplenium ruta-muraria L. (fig. 18).

Bilateral, ovoid, average size 36 × 48 μ, ranging from 30–45 μ × 43–55 μ. Spore covered by a thin convolute perispore forming a more or less undulate margin and bearing on the surface fine setae.

The spores of this species are described and figured by Karpowicz (1927, Pl. 1, fig. 1).

Asplenium septentrionale (L.) Hoffm.

Bilateral, ovoid, average size 30·2 μ × 41·3 μ, ranging from 27–35 μ × 35–45 μ. Spore covered by a thin perispore membrane, thrown into irregular folds. The spore is smaller but otherwise similar to that of *A. adiantum-nigrum* (fig. 17).

The spores of this species are described by Karpowicz (1927, Pl. 1, fig. 3), Erdtman (1943, fig. 473), and by Gams (1948, fig. 180, 13).

Asplenium trichomanes L. (fig. 15).

Bilateral, ovoid, average size 28·6 × 37·4 μ, ranging from 25–36 μ × 33–45 μ. Spore covered by a thin, much-folded perispore membrane, projecting 5 μ beyond the margin to form a narrow irregularly lobed border.

The spores of this species are described and figured by Leurssen (1889, fig. III, iii, *a–p*) and Karpowicz (1927, Pl. 1, fig. 6).

Asplenium viride Huds. (*A. trichomanes-ramosum* L.) (fig. 16).

Bilateral, rather broadly ovoid, average size 28·8 × 34·2 μ, ranging from 25–33 μ × 30–40 μ. Spore has a thin perispore membrane folded in a coarsely reticulate manner and projecting 10 μ beyond the edge of the spore. The perispore has a fimbriate margin.

The spores of this species are described and figured by Leurssen

(1889, fig. III, iii, *a–g*), Karpowicz (1927, Pl. 1, fig. 5), Hegi (1936, Pl. 1, fig. 16), and by Gams (1948, fig. 180, 15*).

Ceterach officinarum DC. (*Asplenium ceterach* L.) (fig. 19).

Bilateral, ovoid, average size 34·3 × 45·2 μ, ranging from 25–40 μ × 40–57 μ. Spore covered by a thin, deeply folded, winged perispore giving an elaborately convolute appearance. Margin about 10 μ broad, irregularly sinuate. The perispore bears on its surface fine setose processes which can be seen on the margin. The spore is larger than in any species of *Asplenium*.

The spores of this species are figured by Hegi (1936, Pl. 1, fig. 11).

Athyrium filix-femina (L.) Roth (fig. 20).

Bilateral, bean-shaped, average size 24 × 37 μ, ranging from 20–27 μ × 33–44 μ. Exospore coarsely granular; differs from the following two species in the absence of a perispore.

The spores of this species are described and figured by Karpowicz (1927, Pl. 1, fig. 9), Hegi (1936, Pl. 1, fig. 22), Erdtman (1943, fig. 477), and by Gams (1948, fig. 182, 37).

Athyrium alpestre (Hoppe) Rylands (fig. 21).

Bilateral, bean-shaped, average size 25·7 × 36·6 μ, ranging from 20–30 μ × 28–40 μ. Spores covered by a thin and folded perispore, margin narrow, 2–3 μ, irregularly lobed.

The spores of this species are described and figured by Karpowicz (1927, Pl. 1, fig. 10) and Erdtman (1943, fig. 474).

Athyrium flexile (Newm.) Syme

Bilateral, ovoid to spherical, average size 26 × 32·2 μ, ranging from 23–30 μ × 27–40 μ. Spore covered by a thin folded perispore; margin 3–5 μ broad, irregularly sinuate. The spores of this species are very similar to those of *A. alpestre* (fig. 21).

Cystopteris fragilis (L.) Bernh. (fig. 22).

Bilateral, bean-shaped or ovoid, average size 31·4 × 52·2 μ, ranging from 25–33 μ × 40–53 μ. Exospore ornamented with coarse, spinose processes, 5–7 μ long and 3 μ broad at the base; processes spaced about 5 μ apart.

The spores of this species are described and figured by Karpowicz (1927, Pl. 2, fig. 1), Hegi (1936, Pl. 1, fig. 17), and Erdtman (1943, fig. 482).

Cystopteris regia (L.) Desv. (*C. alpina* Desv.) (fig. 36).

Bilateral, bean-shaped, average size 26·5 × 44·3 μ, ranging from 23–30 μ × 40–50 μ. Spore covered by delicate wrinkled perispore which bears on its surface minute acicular processes seen as fine teeth on the margin of the membrane which projects about 5–10 μ beyond the spore.

The spores of this species are described and figured by Karpowicz (1927, Pl. 2, fig. 2) as having sickle-shaped spinose emergences.

Cystopteris montana (Lam.) Desv. (fig. 23).

Bilateral, bean-shaped to ovoid, average size 23·4 × 34·7 μ, ranging from 20–25 μ × 30–40 μ. Exospore ornamented with broad, stumpy processes, 3 × 4 μ, and spaced about 2–3 μ apart.

The spores of this species are described and figured by Karpowicz (1927, Pl. 2, fig. 5).

Cystopteris dickieana Sim

Bilateral, bean-shaped, average size 29·4 × 46·4 μ, ranging from 23–30 μ × 35–52 μ. Spore covered by a thin wrinkled perispore; margin about 5 μ, irregularly sinuate. The spores of this species are very similar to those of *C. regia*, though the perispore here is apparently smooth in contrast to the muricate surface of *C. regia* (fig. 36).

Woodsia alpina (Bolton) S. F. Gray

Bilateral, ovoid, average size 31·6 × 43 μ, ranging from 25–36 μ × 43–53 μ. Spore covered by a thin irregularly folded perispore; margin 2–3 μ and more or less sinuate. The spores of this species are almost indistinguishable from those of *W. ilvensis* (fig. 24) and are described and figured by Karpowicz (1927, Pl. 1, fig. 15).

Woodsia ilvensis (L.) R. Br. (fig. 24).

Bilateral, broadly ovoid, average size 34·5 × 40 μ, ranging from 25–35 × 30–47 μ. Spore covered by a delicate perispore membrane, wrinkled and folded; margin 2–3 μ and more or less sinuate.

The spores of this species are described and figured by Karpowiez (1927, Pl. 1, fig. 14), Hegi (1936, fig. 24, 1), and by Gams (1948, fig. 181, 24). In the figures of Hegi and Gams the pronounced network illustrated as a feature of the spores is misleading. The perispore membrane may assume a pseudo-reticulate form, but it is very variable.

Dryopteris aemula (Ait.) O. Kuntze (*Lastrea aemula* (Ait.) Brack.) (fig. 27).

Bilateral, ovoid, average size 25·5 × 40·1 μ, ranging from 20–35 μ × 30–45 μ. Spores with a perispore membrane so folded as to form large, pustulate excrescences, the marginal lobes variable in size and shape, about 7–10 μ broad.

Dryopteris cristata (L.) A. Gray (*Lastrea cristata* (L.) Presl).

Bilateral, ovoid, average size 36·5 × 49·2 μ, ranging from 30–40 μ × 45–55 μ. Spores with a deeply folded and lobed perispore, similar in appearance to *D. filix-mas* (fig. 25) though larger. The perispore also is muricate and the margin finely toothed.

The spores of this species are described by Karpowicz (1927, Pl. 3, fig. 1) and by Gams (1948, fig. 183, 41*).

Dryopteris dilatata (Hoffm.) A. Gray (*Lastrea dilatata* (Hoffm.) Presl) (fig. 26).

Bilateral, bean-shaped to ovoid, average size 32·8 × 47·2 μ, ranging from 30–35 μ × 45–53 μ. Spores covered by a thin, delicate perispore exhibiting a few large prominent folds, and furnished with setose processes, 2–3 μ long, closely set together. The setae are clearly visible at the margin.

The spores of this species are described and figured by Karpowicz (1927, Pl. 3, fig. 5).

Dryopteris filix-mas (L.) Schott (*Lastrea filix-mas* (L.) Presl) (fig. 25).

Bilateral, bean-shaped to ovoid, average size 30·2 × 44·3 μ, ranging from 25–37 μ × 40–50 μ. Spores covered by a deeply folded and contorted perispore membrane, the margin appearing in irregular lobes about 10–15 μ broad. Copeland (1947) remarks that in *Dryopteris* the perispore shrinks so that the spores become tuberculate or echinate.

The spores of this species are described and figured by Karpowicz (1927, Pl. 3, fig. 2), Hegi (1936, Pl. 1, fig. 18), Erdtman (1943, fig. 493, fig. 479), and by Gams (1948, fig. 183, 40).

Dryopteris spinulosa (Müll.) Warr (*Lastrea spinulosa* (Müll.) Presl).

Bilateral, ovoid, average size 25 × 41·7 μ, ranging from 20–30 μ × 40–45 μ. Spores covered by a thin, loosely folded perispore bearing fine setose processes. The spores though smaller are similar in structure to those of *D. dilatata* (fig. 26). They are described and figured by Karpowicz (1927, Pl. 3, fig. 4).

Dryopteris villarsii (Bell) Woynar (*Lastrea rigida* Presl).

Bilateral, bean-shaped, average size 31 × 40·5 μ, ranging from 25–35 μ × 35–45 μ. Spores covered by a deeply folded and lobed membrane and almost indistinguishable from the spores of *D. filix-mas* (fig. 25).

Polystichum aculeatum (L.) Roth (*P. lobatum* (Huds.) Woynar).

Bilateral, broadly ovoid, average size 28·5 × 36 μ, ranging from 25–35 μ × 30–45 μ. Spores ornamented with close-set, irregularly shaped processes, giving the margin of the spore a ragged appearance. The spores are similar in size and structure to those of *P. setiferum* (fig. 29).

The spores of this species are described and figured by Karpowicz (1927, Pl. 1, fig. 11) and by Hegi (1936, Pl. 1, fig. 15).

Polystichum lonchitis (L.) Roth (fig. 28).

Bilateral, broadly ovoid, average size 25·3 × 31 μ, ranging from 25–30 μ × 25–35 μ. The spores are furnished with irregularly shaped processes about 5 μ long, some conical in outline and others bifid or truncate.

The spores of this species are described and figured by Karpowicz (1927, Pl. 1, fig. 13), Hegi (1936, Pl. 1, fig. 10), and by Gams (1948, fig. 182, 33).

Polystichum setiferum (Forsk.) Woynar (*P. angulare* (Kit.) Presl) (fig. 29).

Bilateral, ovoid, average size 30 × 41·2 μ, ranging from 25–35 μ × 35–45 μ. The spores are furnished with large irregular projections of various shapes and sizes, mostly about 7–8 μ long; some are pointed, others are truncate, bifid or even trifid.

Thelypteris oreopteris (Ehrh.) C. Chr. (*Lastrea montana* Moore) (fig. 31).

Bilateral, bean-shaped to ovoid, average size 28·5 × 42·6 μ, ranging from 25–30 μ × 40–45 μ. The spores are covered by a thin, delicate and folded perispore membrane, the margin of which, appearing as rather large lobes, may be finely denticulate.

The spores of this species are described and figured by Karpowicz (1927, Pl. 3, fig. 3).

Thelypteris palustris Schott (*Dryopteris thelypteris* (L.) A. Gray) (fig. 30).

Bilateral, bean-shaped to ovoid, average size 31·6 × 44·6 μ, ranging from 30–35 μ × 40–50 μ. The spores are ornamented with spinose processes, 5–7 μ long and 2–3 μ broad at the base, set 5–7 μ apart; they are apparently connected at their base by a delicate web-like network. Holttum (1947), in discussion on the general characters of *Thelypteris*, says that the spores have a winged perispore or the wings may be broken up into small laminae or spines.

The spores of this species are described and figured by Karpowicz (1927, Pl. 3, fig. 6), Erdtman (1943, fig. 482), and by Gams (1948, fig. 184, 45*).

Thelypteris phegopteris (L.) Slosson (*Phegopteris polypodiodes* Fée) (fig. 32).

Bilateral, bean-shaped, average size 22·5 × 35·6 μ, ranging from 20–25 μ × 30–40 μ. Spores with a wrinkled perispore membrane projecting in elongated folds beyond the spore margin up to 10 μ in places.

The spores of this species are described and figured by Karpowicz (1927, Pl. 3, fig. 7), Erdtman (1943, fig. 481), and by Gams (1948, fig. 184, 45).

Gymnocarpium dryopteris (L.) Newm. (*Dryopteris linnaeana* C. Chr.) (fig. 33).

Bilateral, ovoid, average size 23·6 × 32·8 μ, ranging from 20–25 μ × 30–35 μ. Spores covered by a folded perispore membrane forming irregularly shaped lobed protuberances.

The spores of this species are described and figured by Karpowicz (1927, Pl. 3, fig. 8), Erdtman (1943, fig. 480), and by Gams (1948, fig. 184, 44).

Gymnocarpium robertianum (Hoffm.) Newm. (*Polypodium calcareum* Sm.) (fig. 34).

Bilateral, bean-shaped to ovoid, average size 24 × 37·1 μ, ranging from 20–25 μ × 35–43 μ. Spore covered by a deeply folded perispore membrane forming prominent and, in some cases, leaf-like projections beyond the spore surface.

The spores of this species are described and figured by Karpowicz (1927, Pl. 3, fig. 9) and by Gams (1948, fig. 184, 44*).

Polypodium vulgare L. (figs. 35*a* and 35*b*).

Bilateral, bean-shaped, average size 47·7 × 73·3 μ, ranging from 45–50 μ × 70–77 μ. The spores are ornamented with large, irregularly shaped warty excrescences; round the conspicuous apical ridge the protuberances are smaller and transversely elongated; the spore margin is sinuate.

The spores of this species are described and figured by several authors, among whom may be mentioned Leurssen (1889, fig. 32), Karpowicz (1927, Pl. 2, figs. 13 and 14), Hegi (1936, Pl. 1, fig. 23), Erdtman (1943, fig. 483), and by Gams (1948, fig. 180, 11).

It is not the purpose of this paper to discuss the value of the spore as a criterion for the classification of ferns, but reference may be made to a few points of general interest. Both the tetrahedral and bilateral or wedge-shaped form of spore is represented among British species, the latter being more prevalent. There is also a wide range of variation in the sculpturing of the spore wall, but more important, as pointed out by Bower (The Ferns, vol. i, 1923, p. 259), is the presence or absence of a perispore, and, as for ferns in general, the British species may be divided into two groups according to the existence or absence of a perispore. It is absent in Ophioglossaceae, Osmundaceae and Hymenophyllaceae, but in the comprehensive family Polypodiaceae the perispore is inconstant in its appearance. Although it may be described as a general feature of most British species referred to this family, it is remarkable that in the genus *Athyrium* the perispore is present in *A. alpestre* (fig. 21) but wanting in *A. filix-femina* (fig. 20). In *Thelypteris* a definite winged perispore is present in *T. oreopteris* (fig. 31) and *T. phegopteris* (fig. 32), but in *T. palustris* (fig. 30) it has been interpreted by Holttum (1947) as broken into small parts and reduced to spines. In *T. palustris*, apart from the faint reticulum and the more acutely pointed prickles, the spore has a general resemblance to *Cystopteris fragilis* (fig. 22) or *C. montana* (fig. 23). The more usual winged perispore is absent also in *Polystichum lonchitis* (fig. 28), *P. setiferum* (fig. 29), and *Polypodium vulgare* (fig. 35).

According to Bower (*l.c.*) the perispore " is clearly a feature adopted late in Descent " and although it " possesses a certain value for comparison ", it is evident that it cannot be accepted as a safe criterion in determining affinities.

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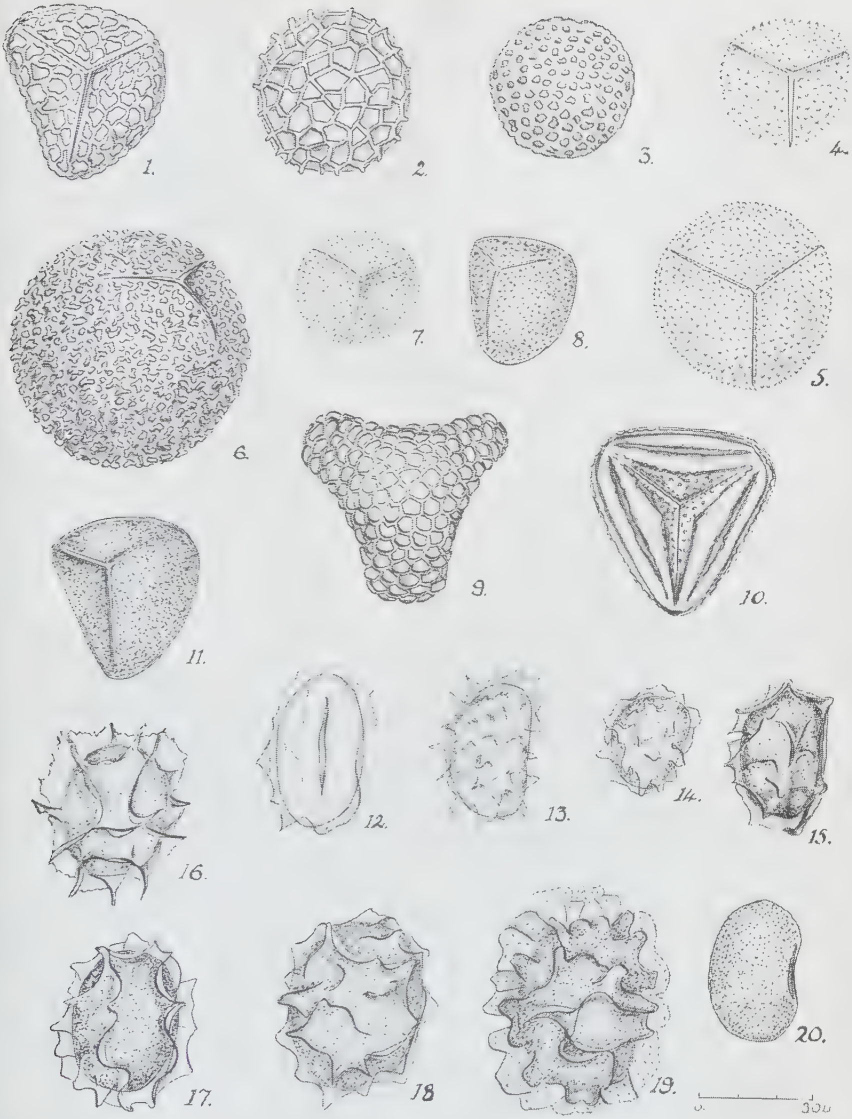
EXPLANATION OF PLATES.

Magnification is × 500.

ap. = apical view. ab-ap. = ab-apical view. l. = lateral view.

Plate XX.

Fig.
1. *Botrychium lunaria* (L.) Sw. (ap.)
2. *Ophioglossum vulgatum* L. (ab-ap.)
3. *O. lusitanicum* L. (ab-ap.)
4. *Hymenophyllum tunbrigense* (L.) Sm. (ap.)
5. *H. peltatum* (Poir.) Desv. (ap.)
6. *Osmunda regalis* L. (ap.)
7. *Trichomanes speciosum* Willd. (ap.)
8. *Pteridium aquilinum* (L.) Kuhn (ap.)
9. *Cryptogramma crispa* (L.) Hook. & Bauer (ab-ap.)
10. *Anogramma leptophylla* (L.) Link (ap.)
11. *Adiantum capillus-veneris* L. (ap.)
12. *Blechnum spicant* (L.) Roth (ap.)
13. *Phyllitis scolopendrium* (L.) Newm. (l.)
14. *Asplenium marinum* L. (l.)
15. *A. trichomanes* L. (l.)



Figs. 1–20. Spores of (1) *Botrychium lunaria*; (2) *Ophioglossum vulgatum*; (3) *O. lusitanicum*;) *Hymenophyllum tunbrigense*; (5) *H. peltatum*; (6) *Osmunda regalis*; (7) *Trichomanes speciosum*;) *Pteridium aquilinum*; (9) *Cryptogramma crispa*; (10) *Anogramma leptophylla*; (11) *Adiantum pillus-veneris*; (12) *Blechnum spicant*; (13) *Phyllitis scolopendrium*; (14) *Asplenium marinum*; 5) *A. trichomanes*; (16) *A. viride*; (17) *A. adiantum-nigrum*; (18) *A. ruta-muraria*; (19) *Ceterach officinarium*; (20) *Athyrium filix-femina*. All × 500.

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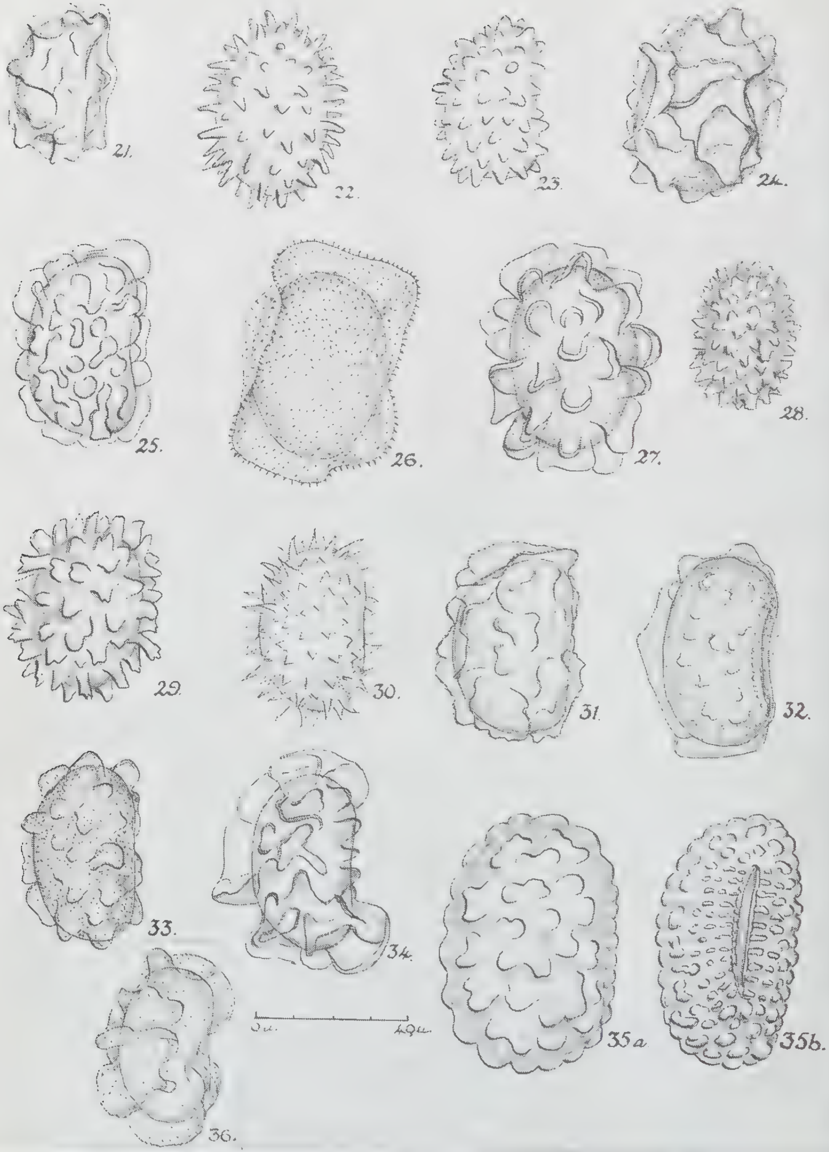
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FIGS. 21-35. Spores of (21) *Athyrium alpestre*; (22) *Cystopteris fragilis*; (23) *C. montana*; (24 *Woodsia ilvensis*; (25) *Dryopteris filix-mas*; (26) *D. dilatata*; (27) *D. aemula*; (28) *Polystichu lonchitis*; (29) *P. setiferum*; (30) *Thelypteris palustris*; (31) *T. oreopteris*; (32) *T. phegopteri* (33) *Gymnocarpium dryopteris*; (34) *G. robertianum*; (35*a* and 35*b*) *Polypodium vulgar* (36) *Cystopteris regia*. All × 500.

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Fig.
16. *A. viride* Huds. (l.)
17. *A. adiantum-nigrum* L. (l.)
18. *A. ruta-muraria* L. (l.)
19. *Ceterach officinarum* DC. (l.)
20. *Athyrium filix-femina* (L.) Roth (l.)

Plate XXI.

Fig.
21. *Athyrium alpestre* (Hoppe) Rylands (l.)
22. *Cystopteris fragilis* (L.) Bernh. (l.)
23. *C. montana* (Lam.) Desv. (l.)
24. *Woodsia ilvensis* (L.) R. Br. (l.)
25. *Dryopteris filix-mas* (L.) Schott (l.)
26. *D. dilatata* (Hoffm.) A. Gray (l.)
27. *D. aemula* (Ait.) O. Kuntze (l.)
28. *Polystichum lonchitis* (L.) Roth (l.)
29. *P. setiferum* (Forsk.) Woynar (l.)
30. *Thelypteris palustris* Schott (l.)
31. *T. oreopteris* (Ehrh.) C. Chr. (l.)
32. *T. phegopteris* (L.) Slosson (l.)
33. *Gymnocarpium dryopteris* (L.) Newm. (l.)
34. *G. robertianum* (Hoffm.) Newm. (l.)
35*a*. *Polypodium vulgare* L. (l.)
35*b*. *P. vulgare*. (ap.)
36. *Cystopteris regia* Desv. (l.)

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